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Erratum: The review of *Historical Perspective* and the *Independent Status of Comparative Psychology*, Volume 1, Number 2, (E. Toland (ed.), Hillsdale, NJ, 1987) was written by Grant Kenyon, The Witchita State University, Witchita, Kansas, USA 67208-1595.

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PSYCHOBIOLOGICAL ASPECTS OF THE ACCELERATION OF POSTEMBRYONIC DEVELOPMENT IN THE ASYNCHRONOUS BREEDER, PIED FLYCATCHER *(FICEDULA HYPOLEUCA)*

S.N. Khayutin, L.P. Dmitrieva and L.I. Alexandrov

ABSTRACT: The nest behavior of the pied flycatcher nestlings was studied in the artificially formed broods. Each of two groups of nestlings with an age range of four days were studied. Under optimal food conditions, the last of the nestlings to appear shortened the incubation period by 20-25% so that the whole brood fledged relatively synchronously. During the first half of nest life in the mixed broods younger nestlings got food mainly due to their constant motor activity, manifested in unceasing spontaneous begging, resulting from the constantly increased level of feeding motivation. During the second half of the nest life younger nestlings, due to their high activity level, get even the greater amount of food than the elder chicks. The long-lasting contact of the nestlings of both age groups is necessary for the selectively accelerated development of sensory and motor components of functional systems of early behavior that ensure the survival of younger nestlings and their fledging, synchronous with the older ones. It is suggested that all factors promoting the accelerated development of younger nestlings are present in the natural habitat.

Numerous investigations of the ontogeny of early forms of behavior in animals with different ecological adaptations have shown that late embryonic and early postembryonic sensory experience greatly influences their behavioral organization. Studies of newly-born mammals have demonstrated the necessity of early stimulation for the development of selective attention as well as for the maturation of the respective information processing systems (Creighton and Tees, 1975; Imbert and Buisseret, 1975). Sarrow, et. al. (1972) found that the odor of male mice stimulates ovulation in young females and reduces significantly the time of their sexual maturation. Moreover, additional physical and social contact in the mouse colony accelerates sexual maturation by 18-20% compared to control isolated mice (Drickamer, 1974). The accelerated development of sexual behavior in male rats was observed under the influence of specific olfactory, tactile, visual and auditory stimulation

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by others (Gruendel and Arnold, 1974). We consider that set of influences to be a social one.

The accelerated development of different functions under the influence of additional specific afferentation is much more pronounced in avian ontogeny. In experiments with laughing gull chicks Impekoven (1976) discovered that exposing embryos to adult conspecific signals, characteristic of the incubation period, resulted in the appropriate reaction by one-day-old chicks to these signals, unlike the incubator bred gulls that started to respond to these signals much later. Adam (1975) found a significant effect of acoustic as well as light stimuli on the development of chicken embryos—they hatched earlier. Even 10 hours of light stimulation (with flashes or with constant light) reduced significantly the duration of the incubation period in chickens. Stimulation during the first week and between days 17 and 20 proved to be the most effective (Siegel et. al. 1969). Acoustical stimulation (clicks) during the last few days of incubation synchronized hatching in quail broods (Vince, 1966, 1968).

Stimulation of avian embryos at late stages of development with the attraction calls of adults or with sounds imitating these calls, accelerated and synchronized hatching in many orders of precocious and in some semiprecocious (grebes, rails, oystercatchers) birds (Vince, 1969, 1973; Impekoven, 1971; Tikhonov, 1986). The most pronounced capability of hatching synchronization is that of the rhea (Vlack and Vlack, 1985; Tikhonov, 1986). The eggs are laid during 3-14 days, incubation is started with the second or third egg laid in the clutch, but all nestlings, nevertheless, hatch synchronously with intervals of 1.0-2.5 hours. The maximal "acceleration" in rhea embryos may reach seven days. Investigations have shown that the "younger" embryos are stimulated during incubation by the clicks, produced by the "elder" embryos at the final stage of incubation and with the signals of the incubating rhea males. The synchronous hatching in precocious birds is a basic condition for the brood to leave the nest region as soon as possible.

In some semiprecocious (gulls, auks, storks), and in most altricial bird species synchronous hatching is almost never observed. The degree of asynchrony varies from few hours to 4-5 days (Clark and Wilson, 1981).

Few theories have been proposed to explain the adaptive value of asynchronous hatching. The most commonly accepted one is the hypothesis of adaptive brood reduction (Lack and Lack, 1951; Lack, 1954). It treats asynchronous hatching and the resulting difference in the size of the young as an adaptation to match the size of the brood to the available food resources. In the species utilizing the brood reduction strategy, the relation of the original clutch size and the number of the fledged nestlings may be considered as an indication of the gradual

process of adaptation to the food conditions including two phases: a) asynchronous hatching, preadapting the brood to the possible future reduction, and b) selective feeding of the most active and largest chicks, regulating the growth of the young with respect to fluctuations of the food resources.

Clark and Wilson (1981) suggested another interpretation of the asynchronous hatching. In terms of their modal asynchronous hatching is seen from the viewpoint of the breeding success, i.e., the probability of the brood survival. Synchronous hatching is more common among species more subject to predation during the nest period, i.e. open-nesters; it is more "advantageous" for these birds to prolong the period during which they have only eggs in the nest. Nestlings are a demasking factor, attracting the attention of predators to the nest. Such species (approximately 30% of the passerines) usually start the incubation after the last egg is laid, so nestlings hatch more or less synchronously.

Asynchronous hatching is most often observed in hole-nesters with their clutches protected against predators. Considering the variety of nest conditions, Clark and Wilson (1981) selected a few factors affecting the onset of incubation, and thus, the succession of hatching of the young. Northern species start incubation before the clutch is completed to protect eggs from freezing; some species have to start incubation before the last egg will have been laid because of the competition for nest sites, robbing of nest material or the necessity to protect the nest against predators. Asynchronous hatching is most pronounced in the late or repeated clutches, during the period of increasing food deficiency. In the latter case the early onset of incubation and the resulting hatching asynchrony may be considered as the parents' attempt to raise some nestlings before the food resources will become sparse. Gibb (1950) noticed that in late and repeated clutches, egg size grew with each successive egg. This observation does not fit the Lack hypothesis, but it may be explained in terms of the breeding success model as the parents' "attempt" to compensate for the difference between chicks that's due to the asynchronous hatching.

The variety of situations affecting the breeding behavior of birds is not so easy to analyse but the aforementioned facts enable us to state that nest adaptations are formed due to the complicated compromise between differently directed pressures of the selection. Later hatched nestlings due to their small size may, indeed, be involved in the competitive struggle, but the unfavourable position of one or a few nestlings is an inevitable price of brood adaptation. Lori (1968) and Illies (1975) found that parents tend to feed selectively the young with the most widely open beaks. Investigators believe that this "conservatism of parental behavior" is one of the basic mechanisms determining the better chances to survive of the elder nestlings. Also, in several bird species (hawks,

gulls) the younger nestlings' mortality rate is additionally affected by the agressive behavior of older siblings that is directly related to their level feeding motivation (Meyburg, 1974; Dennis and Proctor, 1975).

Thus, asynchronous hatching may sometimes lead to the elimination of the younger chicks in the brood. Their mortality rate, according to different investigators, may vary between 1% (Gibb, 1950) and 55% (Parsons, 1975). The reasons for death may be different but for small passerines it is usually starvation (O'Connor, 1984). Nevertheless, even under the worst food and weather conditions the mortality rate of the later hatched nestlings never reaches 100%.

The duration of the nest period in different avian species varies between 10 and 40 days and does not depend upon the degree of asynchrony of hatching. All siblings (synchronously or asynchronously hatched) fledge, separated by the intervals from few minutes to few hours, during the 10th–40th day of life of older nestlings. Since this is the case nestlings that were last to hatch obviously pass the nest stage of development over a shorter period than their older siblings.

It is believed that nestlings of many species must possess some mechanisms, basic for the accelerated development of sensory and motor components of the main behavioral patterns of the nest period (feeding and defence behavior); normal functioning of these mechanisms provides for a synchronous termination of nest period by all nestlings, whatever the succession of their hatching.

MATERIALS AND METHOD

The data were collected in the Oka-Terrace Biospheric Reserve (120 km south of Moscow) during the study of 30 pied flycatcher (Ficedula hypoleuca) families. They were divided into 4 groups. Groups I consisted of five families in which the nestlings hatched during a single day ("natural synchronous hatching"). Group II included five broods that hatched during 1–4 days ("natural asynchronous hatching"). Group III included five families in which the nestlings were mixed artificially irrespective of the duration of the brood hatching. The last group consisted of 15 families: Four broods were transferred into experimental chambers for a thorough study of nest behavior, 11 others were used for control studies. In groups I–III the following parameters were recorded for each chick: time of hatching (each chick was marked with individual color mark right after birth), the time and the degree of eyes opening, daily changes in body weight and the time of fledging. The nest behavior of four families with eight nestlings in each was constantly (10–14 hours a day) observed. One to two days before hatching, the nests were transferred from the ordinary nest-boxes into experimental ones (without a back wall) that were fixed on the wall of a light-protected experimental chamber which housed a researcher with cameras and tape-recorders. Two experiments

(2 families in each experiment) with mixed broods were designed as follows: In each two families nestlings hatched during one day, but in the first family four days earlier that in the second. A few hours after the last chick of the second family had hatched nestlings were mixed between the two nests, so that each brood contained eight chicks, four of each age group.

The observations of nest behavior of nestlings and adult birds yielded the following data: intervals between feedings of each nestling during each day and all nest life, changes in chick's movements in the nest, factors determining each nestling's probability of receiving food during each day and all nest life. To create an exact reference system for recording the position of the young and parents during feeding, the nest was divided into 12 sectors corresponding to the numbers on a clock face, with zone 12 situated right under the entrance-hole. An additional thirteenth zone was the center of the nest. The probability of a nestling receiving food after begging in a certain zone was calculated in the following way: $p=m/n$, where p is the probability of reinforcement of a feeding reaction of a chick begging in a given zone, i—the number of the zone, m—number of reinforced beggings in the given zone, n—total number of reinforced beggings. The interior of the experimental chamber is shown in Fig. 1.

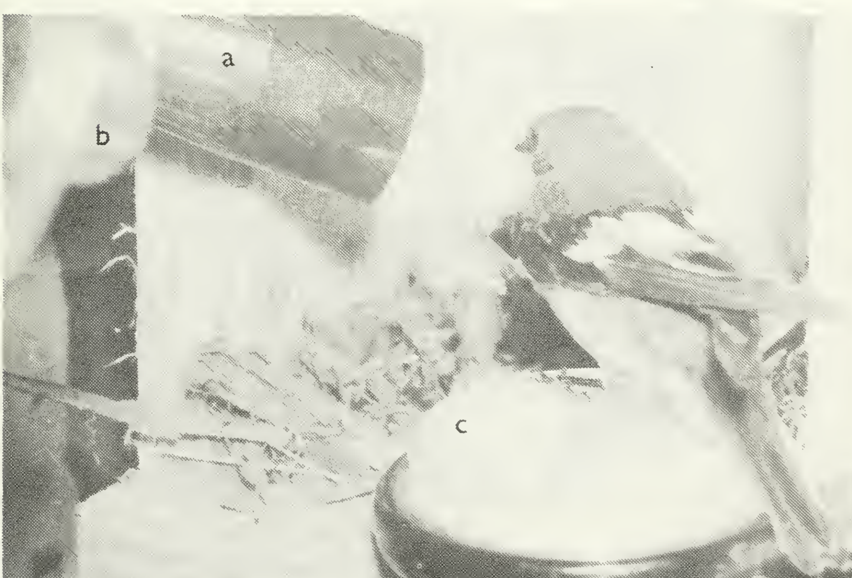

FIG. 1. Interior of an experimental nest-box with the nest of pied flycatcher. (a) Microphone of the tape recorder; (b) microphone of the sound pressure level meter; (c) photoelectric element.

RESULTS.

The analysis of nest behavior of the synchronously hatched nestlings of pied flycatcher revealed that, with respect to the triggering afferentation of feeding behavior, the nest life of the young can be subdivided into distinct stages (Khayutin and Dmitrieva, 1978a, 1981b; Khayutin, 1985; Fig. 2).

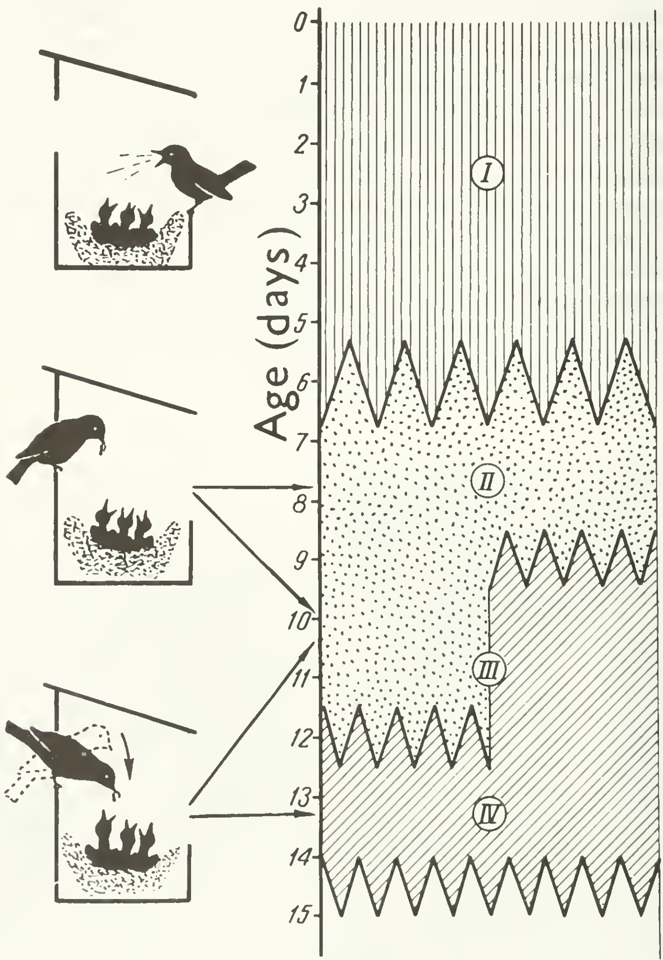

FIG. 2. Periods of nest life as determined by the triggering stimuli of feeding behavior. I. Feeding reactions elicited by the complex of auditory stimuli; II. Feeding reaction elicited by the short-term luminosity change; III. Feeding reaction organized on the basis of two visual stimuli: triggering and guiding ones; IV. Feeding reaction elicited and directed by the silhouette of the moving bird. Figures to the left of the schema—age of nestlings in days.

I. From the moment of hatching until the onset of eye opening, i.e., until day 5-6, begging is elicited by a complex of acoustic stimuli: feet tapping on the wall of the nest-box as the bird arrives, the rustle of the nest material as the bird perches on the edge of the nest and the species-specific "food" call, emitted by a parent (Fig. 3). The analysis of feeding behavior revealed that there were fixed zones in the nest that adults occupied during feeding and zones that were characterized by the maximal probability of begging reinforcement. A statistically equal number of feedings of each nestling during the first half of nest life is determined by a specific behavioral phenomenon—the more or less regular circular shift of the chicks in the nest (Khayutin, 1963, 1985; Khayutin and Dmitrieva, 1976; Best, 1977). The optimal feeding zones are believed to be determined by the position adopted by the parent for feeding the young (always the same for a given bird in a given nest). The position of the adult determines whether food will be placed in the open beak of a nestling that is begging in a certain zone.

II. From day 5-6 nestlings' eyes start to open and, accordingly, the set of stimuli eliciting begging changes. The luminosity change caused by the parent bird's body closing the entrance hole becomes the leading factor in feeding behavior. These luminosity changes are about 1-2 log. units and 100-150 msec long. After the nestlings' eyes open the circular shift of the young loses its even character—they start to move along the luminosity gradient that is determined

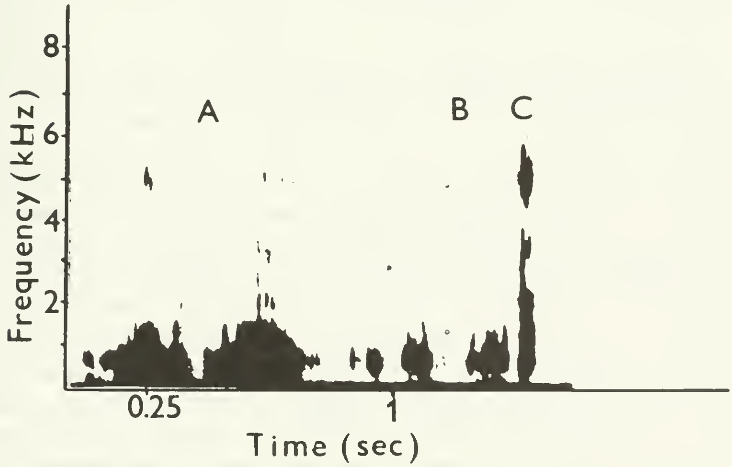

FIG. 3. Sonograms of the signals of adult birds affecting the feeding behavior of nestlings: the sonic complex of feeding. (a) Foot tapping on the nest-box; (b) rustle of nest material; (c) species-specific food call.

by the nest-box construction. At the same time their behavioral repertoire is enriched: the level of vocalization, both background and evoked, increases and the passive-defence reaction appears. The latter consists of the cessation of vocalization and freezing in response to the alarm call emitted by the parents outside.

III. From day 8-9 feeding behavior is modified significantly. Upward neck stretching and beak opening (characteristic of nestlings during the first half of the nest period) is replaced by active food seizure, ie., passive feeding behavior is transformed into active food-acquisition. Chicks turn their heads towards a parent, attacking its beak and snatching away food. It was found that this behavior pattern is organized on the basis of two kinds of visual stimuli: triggering (luminosity change) and guiding (moving silhouette of the adult) ones.

IV. From day 12 and until the fledging of nestlings the moving silhouette of the adult plays the role of both triggering and guiding stimulus. Diffuse luminosity change loses its importance.

Thus, with respect to the change in sensory stimuli that are basic for the occurrence of nestlings' feeding behavior, there are several successive stages separated by 1-2 day transition periods in the nest life of flycatcher young.

The analysis of the behavior of naturally asynchronously (during 3.5-4 days) hatched nestlings confirmed that the adults selectively fed the older nestlings with beaks more widely opened during begging. When nestlings of two age groups (age difference 3.5-4 days, each group including 4 siblings) were experimentally mixed in the same nest, mean intervals between two feedings of the same chick were 13.3 min. for the older group and 37.5 min.—for the younger one. During the two days preceeding the change of nestlings (when each of the broods consisted of 8 siblings of the same age) those intervals equaled 18 min. (Fig. 4, B).

Feeding behavior of nestlings in the two age groups differed significantly. During the first 4 days of life in the mixed brood older nestlings begged spontaneously very rarely, whereas the younger ones demonstrated almost unceasing spontaneous feeding reactions—when the parents were away about 80% of the time was filled with spontaneous begging of one or more chicks. Younger nestlings got food only in two cases: 1) the arrival of an adult coincided with their spontaneous begging, while the sounds accompanying the arrival either failed to elicit a feeding response in the older nestlings or elicited it with too long a latency; 2) when the feedings by two parents were separated by only a vary short interval then the begging of younger nestlings was maintained due to the vocalization of the older ones, responding to the first arrival of the parent. Even these favorable situations, however, did not always

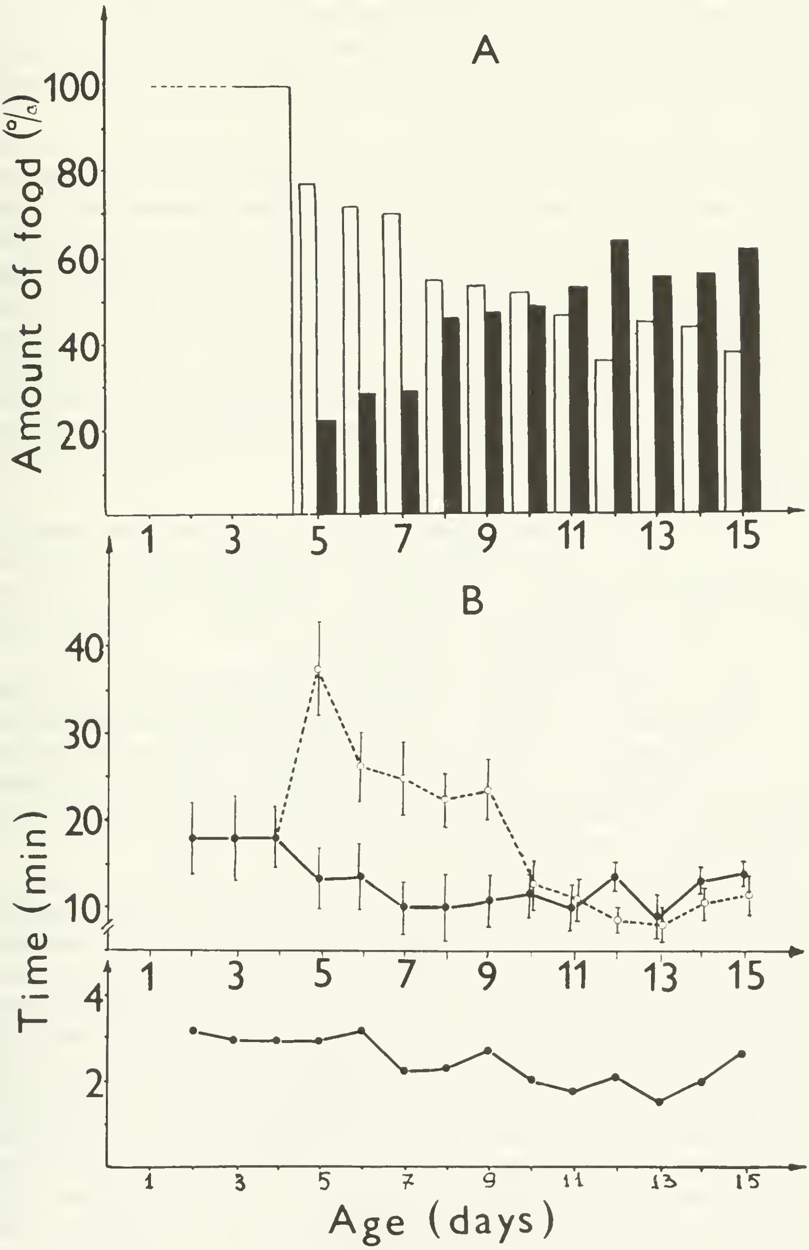

FIG. 4. Distribution of food among the nestlings of two age groups during their life in the mixed brood. (A) Relative amount of food received by the nestlings of older (open bars) and younger (black bars) age groups; (B) mean intervals between feedings of the same chick in the older (solid line) and younger (dashed line) age group; (C) mean intervals between the arrivals of adults with food.

result in the feeding of the younger chicks. In approximately 10% of the cases an adult bird, after a few unsuccessful attempts to feed the younger nestlings, gave food to the older one, who happened to be begging at this time. In other cases, the food was given directly to the older chicks.

Comparison of the daily number of feedings of each chick in the younger age group with that of a nestling of the same age in the natural "synchronous" brood demonstrated that the former received only about 75-80% of their normal food ratio. The analysis of changes in the body weight of the nestlings in the mixed broods proved, however, that during the first days after hatching the body weight of the chicks of the younger age groups is much closer to a normal value than would be expected judging by the insufficient number of feedings they received (Fig. 5). Moreover, unlike the synchronously hatched nestlings that get their food "automatically", younger chicks in the asynchronous broods, to get even a smaller amount of food, have to spend much more energy in frequent, almost unceasing, begging.

Thus the great number of spontaneous feeding reactions, resulting from the increased level of feeding motivation, which, in turn, is due to the 20-25% decrease in the number of feedings, appears to be an important factor helping the younger chicks to get food during their first days of life together with the older nestlings.

Another important factor helping the younger chicks to get food is an interesting modification of the circular shift reaction in the asynchronous broods. It differed from that in the synchronous broods and was quite alike in all 4 mixed nests that were under constant observation. For this reason we will present here the data on the organization of the circular shift in only one brood.

Zones used by the parents for feeding the young were 1 and 11 and did not change even if both parents were in the nest-box simultaneously. As Fig. 6 shows, during the first 4 days (from the moment of hatching until the moment when part of the brood was changed) zones 5, 6, and 7 were optimal for the chicks to get food and zones 1, 9 and 12 were suboptimal. When begging in other zones, nestlings either never got food or got it very rarely. On the morning of day 3 in this brood (the day before the broods were mixed), the full cycle of the shift of a nestling from the optimal zone through all intermediate ones and back to the optimal was 35-37 minutes. During the very first day after the partial change of nestlings the circular reaction shift underwent significant modification. Movements of the younger chicks were relatively independent of the activity of the older ones. As a result, during four days wer could observe two cycles of rotation that overlapped only partially. Younger chicks huddled in the suboptimal zones: in the center of the nest, zones 12 and 1 (Fig. 6, B), and did not leave it, having received food. Their movements were quite local, i.e., they moved one

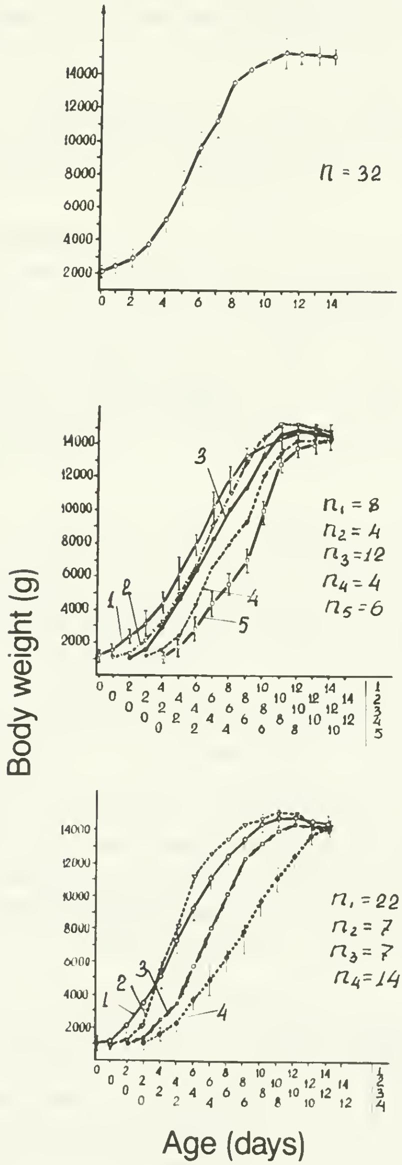

FIG. 5. Changes in nestlings' body weight during the nest life. (A) Natural "synchronous" broods; (B) natural "asynchronous" broods; (C) artificially mixed broods. n—number of nestlings in each age group.

around the other but strictly within this area, while the older nestlings moved all around the nest and sometimes got food in the zones with a low probability of reinforcement. The full cycle of rotation for the older nestlings during the fourth day of their life in the mixed brood (day 8 of life) was 28-30 min. The mean interval between two feedings of the same chick of the younger group had decreased by that time 1.5-fold (Fig. 4, B).

On day 5 of life the eyes of older nestlings began to open. The eyes of younger nestlings opened during day 4 of their life. In spite of this no significant changes in the organization of feeding behavior were observed.

From day 9 of the older nestlings' life the guiding stimulus was included in the organization of their feeding behavior, so their begging was transformed into food-aquisition behavior—now they didn't raise their heads up, but stretched them in the direction of the parent's head, actively attacking its beak even before it would take its place on the nest edge. Since that day, elder nestlings started to get food from the adult that was sitting in the entrance-hole. The distribution of the zones, optimal for begging reinforcement, that was settled during that day is presented in Fig. 6, B.

Younger nestlings also started to get food from the entrance-hole 24-30 hours later (Fig. 6, B). Thus on the 10th day of older nestlings' life two relatively independent rotation cycles merged into one general cycle of movement along the luminosity gradient: the zones located right under the entrance-hole (11,12, 1) became optimal for all nestlings. The mean intervals between feedings of the same chick in both age groups became equal (Fig. 4, B). During this and the following day all nestlings in both age groups received equal amounts of food. Later on, however, mean intervals between two feedings of the same younger nestling became shorter than those for the elder ones. Accordingly, the amount of food received by the younger nestlings exceeded that received by the elders (Fig. 4, A). The higher level of constant movement activity and, therefore, the shorter latency of begging must be the factors ensuring the greater amount of food received by the younger nestlings during the last days of nest life.

The dynamics of the nestlings' body weight during the nest period is described by a S-shaped curve (see Fig. 5). During a good part of nest life the body weight of the chicks that hatched last (Fig. 5, B) is lower than that of their older siblings. The same holds true for the artificially-mixed broods (Fig. 5, C). Body weights of nestlings of different age become equal only during the last days of nest life, when the weights of older nestlings are stabilized or even decreases slightly while the weights of the younger nestlings are still growing. The youngest chicks practically do not have a "plateau" phase. Body weights of the fledglings are equal and do not depend on age. In spite of this, in most of the broods studied

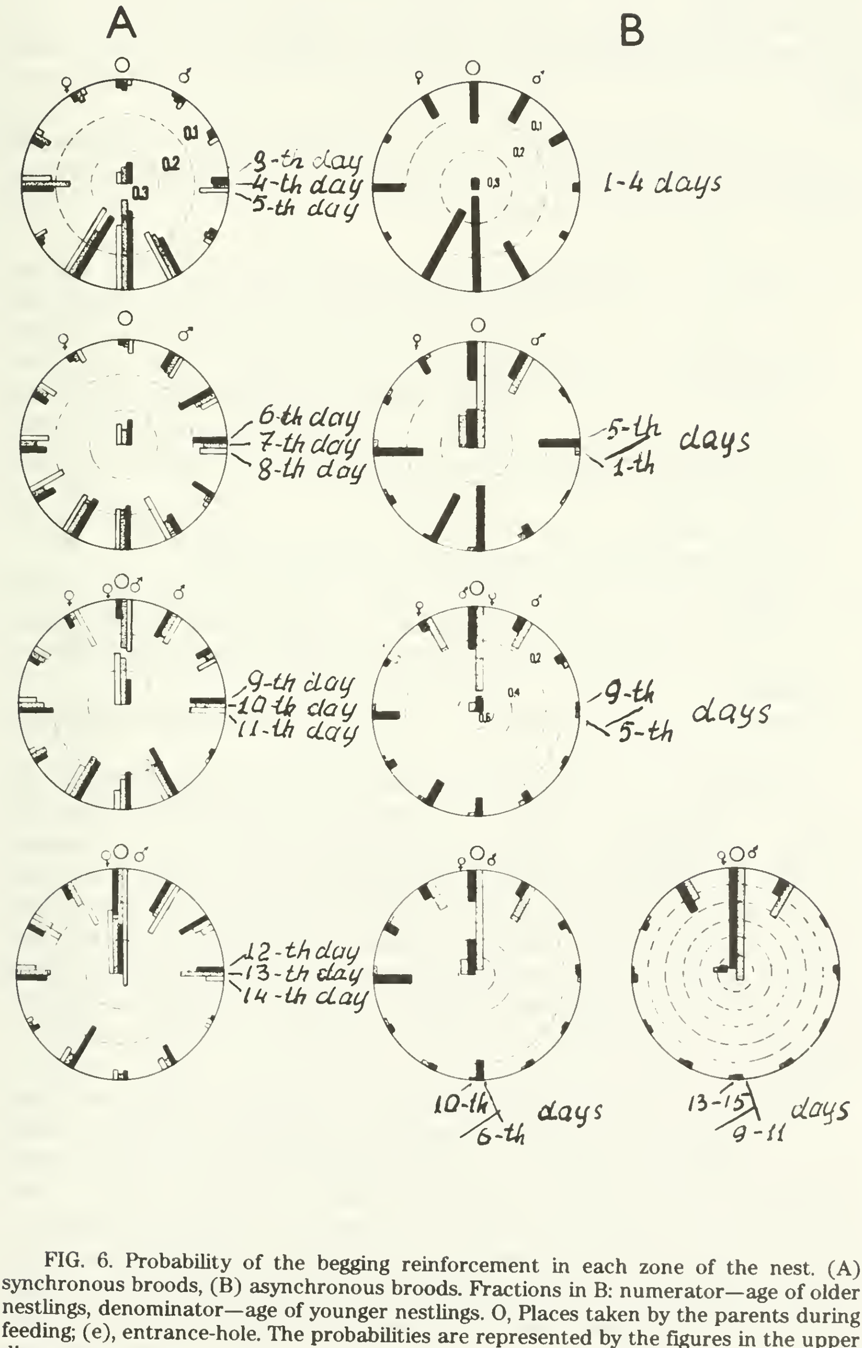

FIG. 6. Probability of the begging reinforcement in each zone of the nest. (A) synchronous broods, (B) asynchronous broods. Fractions in B: numerator—age of older nestlings, denominator—age of younger nestlings. O, Places taken by the parents during feeding; (e), entrance-hole. The probabilities are represented by the figures in the upper diagrams.

with asynchronously hatched nestlings where they could fledge during several hours, the first young to leave the nest were always the older nestlings. Often, right after the very first fledgling had left the next-box, the intervals between the arrivals of the parents with food increased greatly and continued to lengthen as other nestlings were leaving the nest.

Thus, preliminary analysis of our material makes it possible to consider the following factors responsible for the synchronization of fledging of different-aged nestlings:

A. A high level of feeding motivation throughout the entire nest period. Due to this, a constantly increased level of movement activity. At the earliest stage of nest life, this is manifested in the great number of spontaneous beggings, while at the final stage, it is seen in the increased number of stimulus—elicited beggings and in the great number of movements around the nest between feedings. During the final stage this helps younger nestlings to get more food than the older ones.
B. Younger nestlings live in the environment, constantly enriched due to the vocalizations and movements of elder nestlings.
C. Stabilization of body weight of older nestlings (the same for the synchronously hatched chicks) before their fledging. Nestlings that hatch later reach the same weight and fledge without the "plateau" phase.
D. Increased intervals between feedings after the older nestlings fledge.

To estimate the individual role each of these factors plays in this complex an additional study was designed. First of all, counting the number of feedings of nestlings that hatched as late as can be observed in the wild (with maximal possible lag) showed that during nest life each of them received less food than older nestlings or synchronously hatched ones (Fig. 7). Although it is greated during the entire nest life, movement activity does not help younger nestlings to receive normal food rations but it apparently improves both food utilization and the accelerated development of motor components of early functional systems.

In the series of control experiments with eight broods we varied the time of mixed life of differently aged nestlings in the mixed brood. An age difference of 3.5-4 days was created not 10-10.5 days before fledging, as the situation occurs in the wild, but eight, six, four or two days before. It was found that in the first two cases body weights of younger nestlings at the moment of the fledging of the older ones had reached "fledging" value, but, nevertheless, they stayed in the nest after the older ones fledged. In the third case, the difference in body weight between the fledged chicks and those that stayed in the nest was

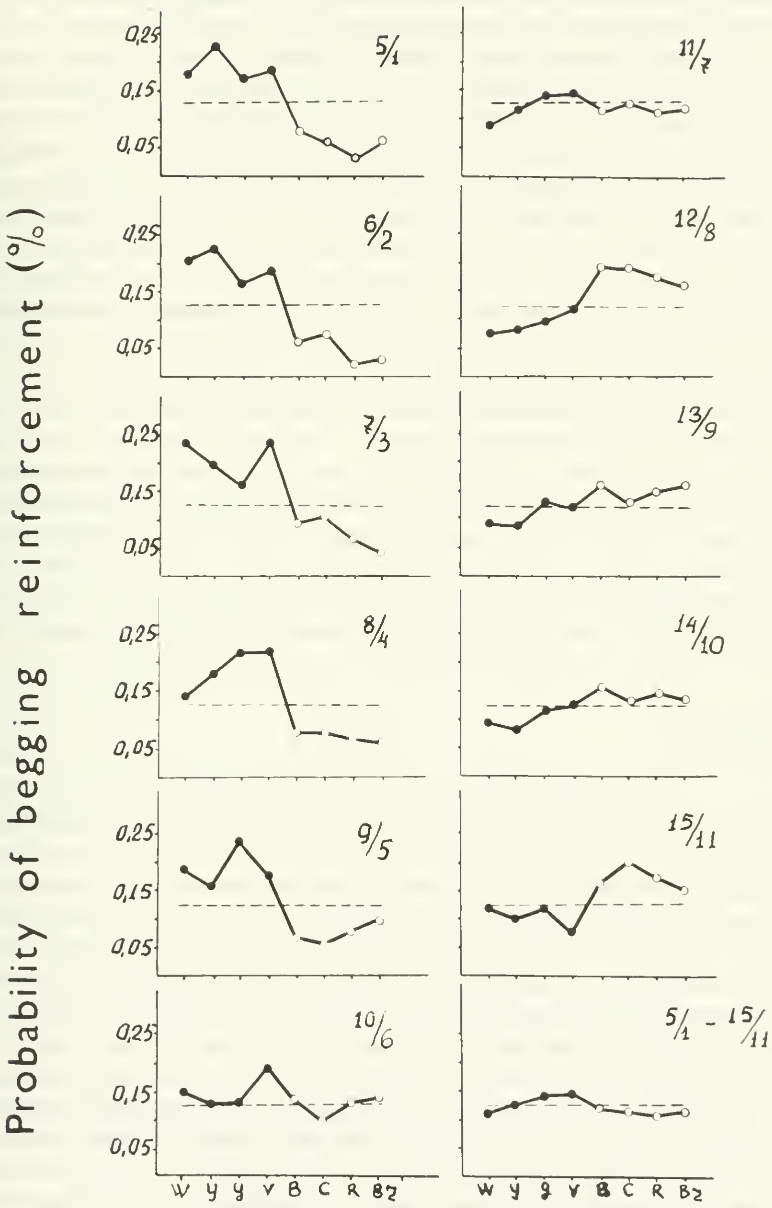

FIG. 7. The probability of getting food for each nestling of both age groups during each day and the entire life of the mixed brood. Ordinate—the probability of getting food for each nestling; abscissa—chicks' individual marks (W, Y, G, V—elder nestlings, B, C, R, Br—younger nestlings). Dashed line marks the level of equal probability to get food. Fraction in each graph: numerator—age of older nestlings, denominator—age of younger nestlings.

statistically insignificant; in the last case body weight of younger chicks was significantly lower than that of the older ones at the moment the latter fledged. Besides, it was found that right after the first nestling had fledged, the mean and individual intervals between feedings increased dramatically. These intervals grew still longer after all older nestlings had left the nest. During the first day after the last older nestling had fledged, the mean interval between feedings of the young remaining in the nest was 47 min., unlike 2.1 min. the day before the fledging, some intervals reaching 2.5-3 hours: they continued to increase until the brood left the vicinity of the nest and adults ceased to feed the chicks in the nest. During the first day after fledging by the older nestlings body weights of the young ones in the nest decreased by 8-10%. An attempt to continue the experiment would have resulted in the death of the chicks.

Thus, the experiments proved that neither "fledging" weight, nor the increase in the intervals between feedings, taken by themselves, determine the premature leaving of the nest. At the same time this study provides another example of the conservatism of parental behavior—adults stop feeding the younger nestlings in the nest after the fledging of the older ones. This, in turn, leads to the hypothesis that the synchronization of the fledging of differently-aged nestlings is also an adaptive factor determining the accelerated maturation of sensory and motor components of the leading functional systems of nest life.

DISCUSSION

Our experiments revealed several behavioral mechanisms ensuring the survival of all nestlings in the brood in spite of their initial differences in age and, accordingly, in the physical state and sensory experience. It must be noted here that the tendencies determining the survival and the synchronization of development are, to some extent, contradictory and equivocal. As it may be inferred from our experiments, the survival of the nestlings, initially lagging behind in the level of their physical development during the first half of the nest life, is insured only by their own activity that compensates even for the conservatism of parental behavior. This conservatism manifests itself in the selective feeding of the chicks with bigger and wider opened beaks, i.e., of the older nestlings.

Our observations are in agreement with those of Illies (1975). He found that the thrush female ignored her own young trying to feed the dummy if it had a wider beak that was constantly opened and if the inner surface of its mouth was more brightly colored. The author proposes that this behavior of the female is inborn and has, under normal conditions, a selective function. An alternative interpretation of the conservatism of parental behavior is suggested elsewhere (Khayutin e. a. 1982).

In our experiments it was found that younger nestlings received the food providing for their survival during the first half of the nest life owing to, first of all, a great number of spontaneous feeding reactions determined by the high level of their feeding motivation. Some spontaneous reactions may, in fact, not be endogenous, but elicited by the sensory stimuli that are subthreshold for older nestlings due to the lower level of their feeding motivation. The influence of the high and low level of motivation on the perception thresholds and the reaction time was proved by many investigations.

Another factor ensuring that younger nestlings will receive food during the first half of their nest life is their constant remaining in the zones with relatively high probability of begging reinforcement. The same observation was made by Lebedeva and Lomadze (1986) who repeated our study, having investigated the artificially-mixed broods of the great tit (*Parus major*). From the analysis of feeding behavior in the "synchronous" broods we inferred (Khayutin, Dmitrieva, 1976) that the principle factor which determines whether a nestling receives food is his begging in the zone of high probability of reinforcement. The present study demonstrated, however, that within the natural limits, the great differences in the ages of the chicks cannot affect the equal distribution of food among all the chicks. In strong opposition to it is the conservatism of parental behavior directed at selective feeding of larger nestlings. Moreover, today we cannot answer the question what makes the younger chicks, huddle in a compact group before their eyes open and immediately afterward, within the fixed region of the nest and not move through all other zones. It may be supposed that this huddling is based on thermal and tactile stimulation.

We call attention to the following fact in our experimental material. In spite of a daily food ration decreased by 20-25% during the first days of the younger nestlings' life, the difference in body weight between chicks of the groups compared does not increase but, on the contrary, has a tendency to decrease, though younger chicks obviously spend more energy because of the great amount of spontaneous begging.

From the point of view of Arshavsky (1975), the increased movement activity of young animals leads to a more effective food utilization that not only compensates for energy losses but also provides for the plastic needs of the growing organism. Saraev's (1974) experiments proved the positive effect of partial undernutrition during limited period on the future growth of animals, their physical activity and an index of food utilization for growth. This author believes this positive effect is due to the influence of physiologically active metabolites formed in the process of undernutrition-induced histolysis.

The increase in movement activity of younger nestlings caused by their constantly increased level of feeding motivation during the first

half of nest life is also observed later on. This must be an important factor helping the younger nestlings obtain a greater amount of food (as compared with older siblings) during the second half of nest life. Moreover, as ensuring the normal physical state of the nestlings, basic for the accelerated formation of sensory and motor mechanisms necessary for the transition to life in the open, synchronous with the older siblings.

Comparison of the stages of maturation of the sensory systems at different ages shows that the progressive shortening of the periods of each stage successively changes the stimuli adequate to elicit feeding behavior.

Comparison of the results of the main series with the control experiments demonstrated that the normal physical maturation of the younger nestlings during the shorter time demands a sufficiently long contact with older nestlings. It is this contact that must create the necessary bases for the selectively-accelerated (heterochronous, according to Anokhin, 1974) formation of the leading sensory and motor capabilities in the younger nestlings. The following factors may be considered as the principal ones, determining the accelerated development of nestlings: their increased movement activity; an additional complex of tactile and thermal influences which is due to the movements of the older nestlings; vocalization of the older nestlings accompanying their begging from the earliest days of life of younger chicks. The complex of these factors, determining the accelerated maturation of sensory and motor components of the functional systems of the chicks' nest life, is considered as a physically and socially enriched environment.

The study of Vlack and Vlack (1985) showed that rhea embryos also needed sensory and social stimulation for normal development. The rhea's incubation period may vary between 29-43 days. The investigators believe the mechanism promoting the accelerated development to be the acoustic communication among embryos confined to the last stage of incubation. The metabolic processes of "older" embryos (oxygen consumption, growth of embryonic tissues) increase exponentially until day 29, then tend to decrease. In the "younger" embryos in the clutch this stage of metabolic decrease may be shortened or eliminated due to embryonic communication, thus promoting the synchronized hatching.

Our earlier data (Khayutin, 1978b, Dmitrieva, 1981b) on the heterochronous development of pied flycatcher nestlings were later confirmed by Lebedeva and Lomadze (1983, 1986) who analysed the natural development of two other passerine species *Parus major* and *P. coereleus*. Applying numerous physiological and behavioral criteria to the natural asynchronous broods they found that the maturation of acoustic and visual analysers and the formation of orienting and defense

reactions in older nestlings of asynchronous broods lag behind, while in the younger chicks they are accelerated as compared with the middle-aged ones. This finding was further developed in a study of a set of morphometric indices (mean growth constants, weight, length of wing and beak, etc.) of great tit nestlings whose relative age was changed by means of transferring them from one nest to another. In one series the nestlings that were older in their own brood were transferred to the broods where they became the younger. The transferred chicks were found to develop according to their new age status as typically young ones—their development was accelerated. In another series younger nestlings were transferred to a still younger brood where they appeared to be the older. As a result, their development decelerated. The authors concluded that the nestlings develop in their new broods according to their new age status, i.e., the pace of their development depends on their age status in the given system and serves the interests of synchronization of the brood as a whole.

The role played by the above-mentioned factors in the accelerated development of sensory and motor components of the principal functional systems of bird nest life is confirmed by many investigations of the effect of sensory deprivation and additional stimulation on the bird embryonic development. Additional stimulation proved to play an important role in the development of the adaptive traits of the embryos of many avian species and to influence significantly the nestlings' behavior after hatching. The experiments of Gottlieb (1968) who paralysed chicken embryos at the early stage of development demonstrated the necessity of movement activity, that is, from the author's viewpoint, the main form of stimulation that muscles and skeleton demand for their normal development.

Thus, our results indicate that the pace of maturation of the sensory and motor components of the early behavioral acts' systems may be determined, to a great extent, by the changed environmental factors. The succession of the maturation of sensory mechanisms must be genetically determined (Gottlieb, 1971) whereas the pace of this maturation is apparently subjected to the influence of physical and social environmental conditions. At the same time, the sensory-enriched environment created by the activity of elder nestlings is the necessary natural factor promoting the accelerated development of the younger chicks.

These mechanisms are to some extent natural for the flycatcher species. The aforementioned studies by many researchers prove that in many species the hatching of the clutch may take as many as several days. Our own data show that the flycatcher is not an exception to this tendency. In other words, under natural conditions the nestlings that were the last to hatch and that, accordingly, lag behind in their physical state and sensory experience, have the mechanisms for the

accelerated maturation of the sensory and motor components of the main nest-life functional systems functioning, thus matching these systems to the level of those in nestlings that hatched earlier.

From our point of view, our results which demonstrate the significant effect of additional stimulation on the accelerated maturation of a number of functions in the developing organism may be best interpreted in terms of the concept of the ontogenetic consolidation of functions (Anokhin, 1964, 1974; Shuleikina, 1973; Kiselev, 1978). Embryogeny is considered by this concept not only as a stage of development of this or that functional system but at any moment as a stage of a certain dynamically developing condition of readiness to realize these systems. For at certain stages of ontogeny, the immaturity of functions is manifested not in the inability to perform them but rather in the fact that "the given function needs some additional facilitating influences to manifest itself" (Shuleikina, 1973, p. 285). It is important to stress here that the degree of maturity of the central structures at the final stages of the embryogeny and at early stages of postembryonic development is not the absolute determinant of the ability of the executive mechanisms and systems to function. An important role is played here by the consolidating effect of additional and probably specific stimulation on the final arrangement of a system, i.e., on its functional readiness to be performed. The present study demonstrated that the factor consolidating and accelerating and facilitates the formation of sensory and motor mechanisms of the leading functional systems of early avian behavior is the specific acoustical, visual and tactile stimulation. It was also found that the synchronization and acceleration of the development of sensory and motor components of the main functional systems under the influence of a specifically enriched environment is the necessary factor for the progressive acceleration of the change of developmental stages and the obligatory factor of systemogenesis (term after Anokhin, 1964, 1974). In connection with this the concept of development of the early behavioral functional systems may be extended to include also the supraorganismic level with the obligatory consideration of mutual social influences among individuals in the micro- and/or macropopulations.

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PSYCHOPHYSICAL CONTEXT EFFECTS IN CHICKENS GALLUS GALLUS DOMESTICUS *(HUBBARDS)*

Barbara Zoeke, Viktor Sarris, and Giovanni Hofer

ABSTRACT: A quantitative frame-of-reference *(FR)* model that has been successfully tested in humans was examined in generalization experiments with chickens. In Experiment 1, three groups of two chickens each were trained to discriminate between cubes different in volume and tested with a series of cubes with volumes either below, surrounding, or above the training stimuli. The obtained psychometric functions support the assumption that asymmetrical testing after two stimulus-two response training leads to the changes predicted by the *FR* model. In Experiment 2 shifts in the context defining the test series were administered by gradually enlarging the distance between training and test stimuli. While context effects were found in both experiments these were more pronounced in Experiment 2. The results support the general hypothesis that perception in animals undergoes context effects similar to those obtained in human subjects.

GERMAN ABSTRACT: Psychophysikalische Kontexteffekte bei Küken (Hubbards). — Ein quantitatives Bezugssystemmodell, das sich zur Voraussage reiz- und erfahrungsbedingter Kontexteffekte im Human-versuch bewährt hat, wurde in Generalisationsversuchen mit Küken überprüft. In Experiment 1 wurden sechs Küken trainiert, zwei singulär gebotene Würfel unterschiedlichen Volumens mit zwei alternativen Reaktionen zu beantworten. Im anschließenden Generalisationstest wurden jeweils zwei der Tiere unter je einer der drei Testbedingungen getestet (Würfelserien, die in Relation zu den Trainingsreizen entweder tiefer oder höher auf der Reizskala lagen oder die Trainingsreize symmetrisch umgaben). Die resultierenden psychometrischen Funktionen belegen, daß asymmetrische Testung nach einem "two-stimulus two response training" zu den Änderungen des Antwortverhaltens führt, die das Bezugssystemmodell voraussagt. In Experiment 2 wurden sechs Küken trainiert und mit Reizserien getestet, deren Distanz zu den Trainingsreizen schrittweise vergrößert wurde. Unter diesen Bedingungen zeigten sich stärkere Kontexteffekte als in Experiment 1. Die Daten beider Experimente stützen die generelle Annahme, daß psychophysikalische Kontexteffekte nicht nur beim Menschen, sondern auch bei Tieren auftreten.

The basic assumption underlying definitions of psychophysical context effects is that perception and judgment are relational in character so that responses to an individual stimulus depend not only on its absolute attributes but also on characteristics of the situation, the context in which the stimuli are presented. Consequently, the same stimulus may be over- or underestimated in different stimulus contexts.

This relativity of stimulus-response *(S-R)* relationships is well documented not only in studies employing a frame-of-reference *(FR)*

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approach but also within the stimulus-generalization paradigm as applied to the judgmental behavior of humans (James, 1953; Johnson, 1949a, b; Thomas & Jones, 1962). The typical results obtained here are lawful changes in *S-R* functions that are not predicted from assumptions of *S-R* theories but accounted for readily by *FR* models. Whereas these findings are experimentally well established in humans, the meagre literature on *FR* effects in animals has been, so far, either silent or controversial (Thomas, 1974; Zoeke & Sarris, 1983).

The aim of our present studies was the comparative investigation of psychophysical context effects in animals. The studies were guided by a *FR* model that has been successfully tested in humans using a two stimulus-two response discrimination followed by asymmetrical generalization testing (cf. Thomas & Jones, 1962; Sarris & Zoeke, 1985; Zoeke & Sarris, 1987). Employing this method we predict changes of the form of psychometric functions depending on the context conditions and the subjects experience with the stimuli. The 50% point on such psychometric functions, the stimulus value at which the two response frequencies are equal, may be used as an indicator of these changes (*P*oint of *S*ubjective *I*ndifference, *PSI*; cf. Sarris, 1971). The prediction reads as follows:

$$PSI_n = (k\,PSI_{train} + n\,PSI_{test}) / (k + n), \qquad (1)$$

where PSI_n means the *PSI* for the n-th test session, PSI_{train} the *PSI* of the training stimuli, and PSI_{test} the *PSI* of the test series used; k is an empirical weighting factor, reflecting the effects of experience with the training stimuli; n means the number of times the series is presented.

This *FR* model has been tested in humans ranging in age from 3 to 85 years. The results support the suggested model and show particularly that the slope of gradients obtained with continued testing depends on stimulus conditions (e.g., the distance between training and test stimuli on the stimulus scale used) as well as typical learning variables (e.g., amount of training, practice with the test stimuli). The slope of the gradients depends also on the age of subjects. Gradients obtained from the kindergarten children change about three times as fast as those obtained from adults. Age dependent changes may reflect to some degree the greater preexperimental experience adults have with judgments and stimuli (Zoeke & Sarris, 1987).

The question as to whether and under which conditions animal perception can be experimentally demonstrated to be context-dependent, i.e. to be relative, has been discussed for almost 70 years. Studies of transposition provided the experimental starting point for this controversy. Gestalt theorists have interpreted transposition data as perception of stimulus relations (Kohler, 1918), *S-R* theorists, following Spence (1937), have interpreted them as resulting from summation of excitatory and inhibitory processes. Despite a flood of very suggestive

investigations within the last few decades, this controversy has not yet been resolved (Reese, 1968). More recently, *FR* models were applied to generalization studies employing asymmetrical testing procedures (Thomas & Barker, 1964; Thomas, 1974; Zoeke & Schuermann, 1981). Although the results of Thomas & Barker (1964) did not allow an interpretation in terms of contextual effects, the studies of Thomas (1974) and Zoeke & Schuermann (1981) showed context effects, at least under one of their test conditions. Thomas (1974) made the assumption that the amount of training animals require for the acquisition of discrimination has an important influence on the occurrence of contextual effects (see also James, 1953). Summarizing these results, psychophysical context effects in animals are expected to occur but the changes in psychometric functions should be slower than in humans. Therefore, according to the *FR* model the empirical weighting factor k reflecting the amount of practice with the training stimuli should be higher in animals than in humans.

EXPERIMENT 1

Our first study was directed to a comparison of psychophysical context effects in animals and humans using an asymmetrical generalization testing procedure.

Method

Animals. — Six chickens *(Hubbard)* approximately seven weeks old at the beginning of the experiment, served as subjects. The chickens were kept in individual cages but were allowed to run freely in a scratching pen for about two hours after their daily test session. Food was withheld for 18 hours prior to testing. Water was continuously available in the home cage.

Apparatus. — The computer controlled apparatus permitted the successive presentation of three-dimensional objects. As Figure 1 shows the apparatus consisted of a test and a waiting box divided by an automatically controlled gliding door. Stimuli were presented in front of a 60 x 60 x 60 cm wall on which two pecking keys and two food magazines were fastened, one to the left and the other to the right of the stimulus. The objects were fixed underneath the test box, each on an individual plate, located on a rotatable wheel (diameter: 165 cm). A motor turned the wheel to the correct position, then the plate with the appropriate object was lifted hydraulically into the opening in the floor of the test box (see Figure 1, bottom).

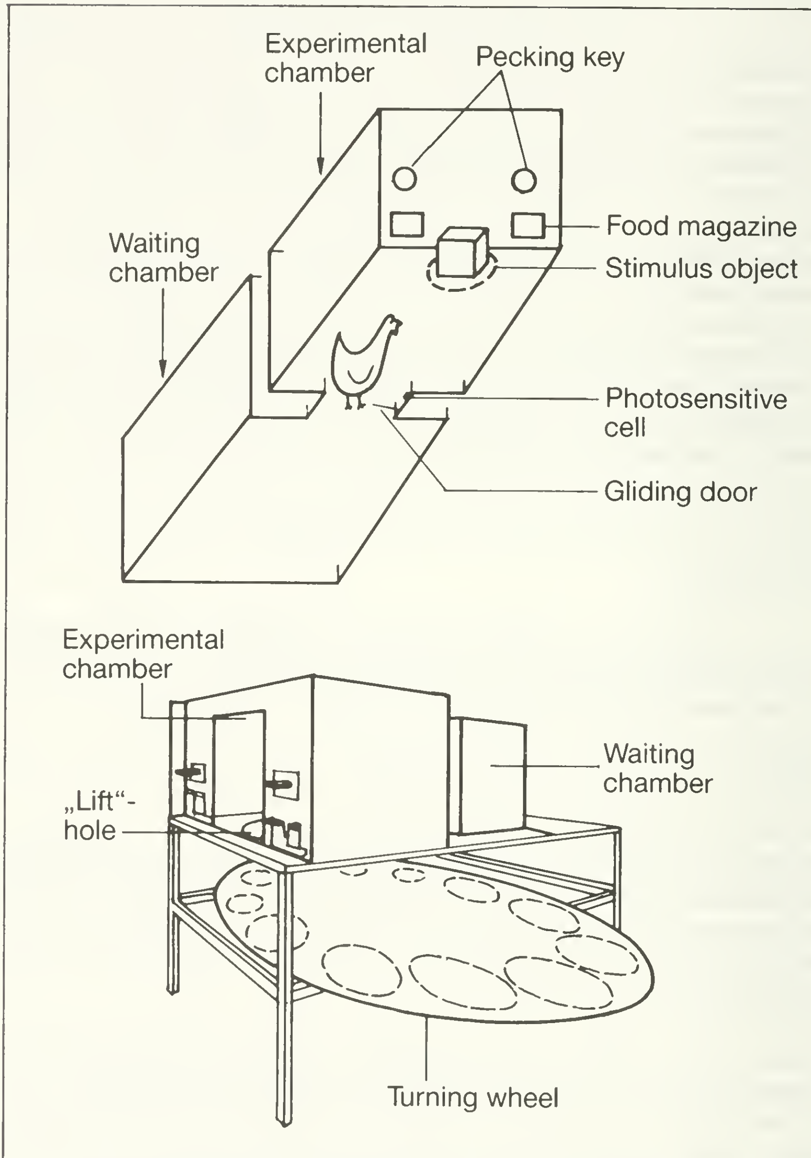


Figure 1

Schematic view of the apparatus used for three-dimensional object presentation. — *Top:* Test and waiting box with the singularly presented cube and two pecking keys and food magazines. *Bottom:* Details of the automatic stimulus presentation. The objects are fixed underneath the test box each on an individual plate on a turning wheel. A motor turns the wheel in the correct position, then the plate with the randomly chosen object is lifted hydraulically into the test box.

Stimulus material. — The stimuli were orange cubes differing in volume in equal logarithmetic steps. All subjects were trained with the same pair of training stimuli (TS), a 215 ccm and a 608 ccm cube, but tested with three different test series. Table 1 shows the physical measurements of training and test stimuli. The test stimuli were equally spaced on a log scale with the geometric mean of the two training stimuli defining the midpoint of the null test series, C_O. For the small contextual series, C_1, the geometric mean of the training stimuli was the largest of the test stimuli. For the large contextual series, C_2, this was the smallest of the test stimuli.

Table 1

Set of training and test stimuli used (general design logic)

Physical Scale Volume (in ccm)	45	64	90.5	128	181	256	362[a]	512	724	1024	1448	2048	2896
Training Stimului						215		608					
Null Test Series (C_0)				128	181	256	$\boxed{362}$	512	724	1024			
Small Contextual Test Series (C_1)	45	64	90.5	128	181	256	$\boxed{362}$						
Large Contextual Test Series (C_2)							$\boxed{362}$	512	724	1024	1448	2048	2896

Note. Subjects are trained with two successively presented training stimuli (*TS*) and tested with different test series either symmetrically (C_0) or asymmetrically distributed to the *TS* (C_1, C_2).

[a]The stimulus surrounded by black lines is middle-sized under C_0, the largest and C_1, the smallest under C_2.

Procedure. — The experiment included three phases for each subject: (1) Key training, (2) discrimination training, and (3) generalization testing. After key training the subjects were trained to peck key 1 if TS 1, the 215 ccm cube was presented, to peck key 2 if TS 2, the 608 ccm cube was presented. Daily training sessions consisted of 50 trials. The stimulus sequence was randomly determined each day with the restriction that each stimulus was presented with equal frequency.

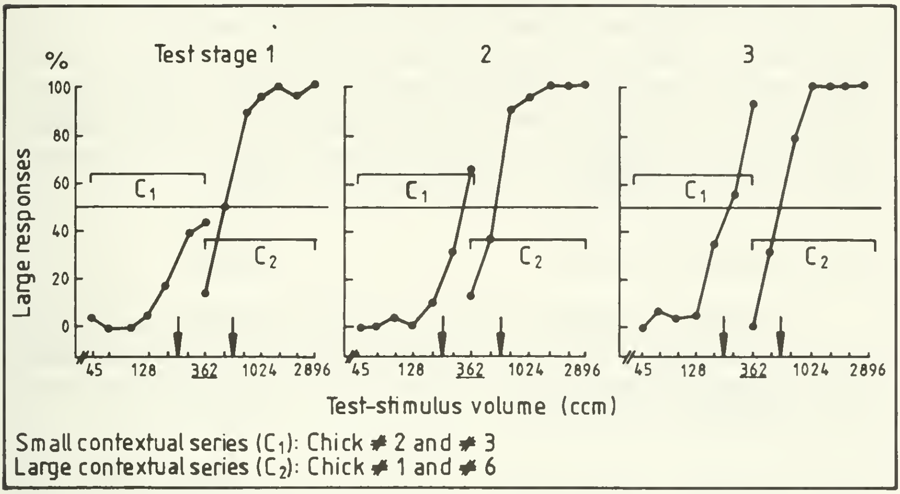
At the start of each trial the subject was held in the illuminated waiting box while a cube was positioned in the test box. Then the light was turned off in the waiting box while the light in the test box was turned on and the gliding door was opened. Following this brightness shift, the subject entered the test box. If it pecked the correct key this key choice was reinforced by access to the food magazine for three seconds. The test box was then darkened, the waiting box was illuminated

again, and so forth. Darkness immediately followed an incorrect key choice and the same stimulus was presented again after six seconds.

After reaching the learning criterion (95% correct choices for three successive training sessions) the six subjects were assigned randomly to the three test conditions. Each series was presented six times daily during six test days. All choices were reinforced.

Results and Discussion

The average number of trails required for reaching the learning criterion was 2230 (SD = 579). The top panel of Figure 2 shows the results of the generalization tests. The proportions of responses to the key that was correct for the large training stimulus ("large" responses) are shown for the two context conditions (C_1, C_2) separately for test stages 1, 2, and 3. Pairs of test sessions, a total number of 12 responses for each of the test stimuli were combined to form the three test stages. These data support the predictions of the microgenesis of context effects over test stages (bottom panel of Figure 2). During test stage 1 subjects tested with the small context series (C_1) were expected to use the response "large" infrequently while those tested with the large context series (C_2) were expected to use this response frequently. These results correspond to those expected by classical psychophysics. However, according to the *FR* model, as testing progresses (test stage 2, 3, . . .) the same stimuli are increasingly judged either as "large" or "small" depending on the test series used. As a consequence, the *PSI* shifts towards the test-series center C_1 or C_2, respectively (see also Equation 1). Note, that the 362 ccm cube, physically equal for all test series, is responded to as "large" on approximately .5 of the trials at the beginning of the test phase (test stage 1), but this proportion shifts towards either "large" or "small" by the third test stage. An analysis of the proportion of "large" and "small" responses for the 362 ccm cube for each test stage under the two context conditions indicates, as expected, that the differences found between C_1 and C_2 are not statistically significant at test stage 1, but highly significant ($p < 0.001$) at test stage 2 [$\chi^2(1,N = 48) = 15.02$] and at test stage 3 [$\chi^2(1,N = 48) = 37.00$]. At the same time, two trend tests, done for the changes of *PSI*-values over the three test stages (cf. Ferguson, 1965), indicate that the *PSI*-values decrease under C_1 ($z = 1.73$, $p < 0.05$) and increase under C_2 ($z = 2.23$, $p < 0.02$). Furthermore, tests of trend differences (cf. Lindquist, 1953) comparing the predicted and observed *PSI* trends under C_1 and C_2 show that Equation 1 predicts the observed changes appropriately. In fitting the model, the empirical weighting factor k was found to be 34 under C_1 and 29 under C_2, $F(2,3) = 0.55$ and $F = 0.30$., respectively. These differences are insignificant as expected.



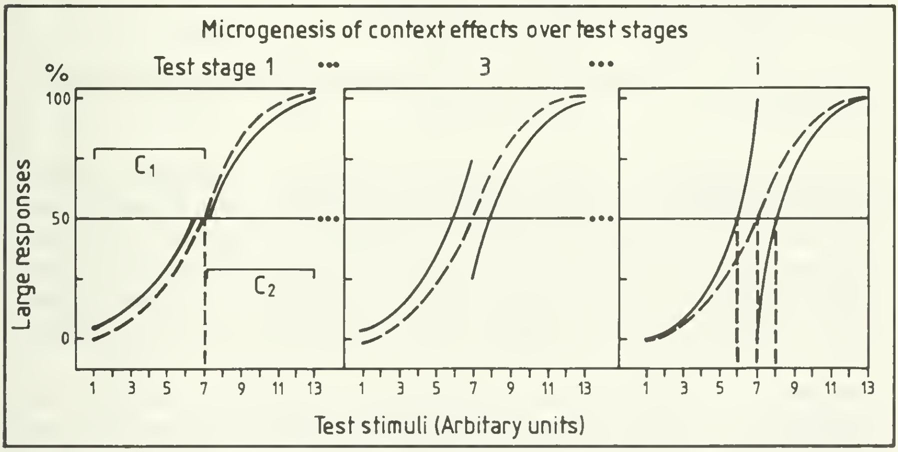


Figure 2 (upper)

Changes of S-R functions over test stages. — As predicted (see *Fig. 1*) *Ss* tested with a small context series (C_1) use in the beginning very few "large" responses, the other group (C_2) many (test stage *1*). These reaction rates increase and decrease over test stages (test stage *2*, *3*). At test stage *3* one and the same stimulus (volume of *362* ccm) is judged either as "small" or as "large" under C_1 versus C_2 context.

Figure 2 (lower)

Hypothetical microgenesis of context effects over test stages. — *Dotted lines:* Absolute psychophysical function valid for the whole stimulus scale. *Solid lines:* Psychophysical functions undergoing response changes by the different context conditions. Whereas in the first test stage (n=1) subjects tested with a small context series (C_1) use very few "large" responses, the other group (C_2) many, these reaction rates change over the test experience (test stage n=3 to n=i) physically equal stimuli are increasingly judged either as "large" or as "small" according to the context series used.

These data show, as predicted by the *FR* model, that context effects in animals do appear. However, the empirical weighting factor *k* expressing the slope of changing gradients (1/k) was about 10 times higher with the present subjects than previously found in human adults, and about 30 times higher than found in kindergarten children (Zoeke & Sarris, 1987). In addition, ascending test series (C_2) seem to produce larger contextual effects than descending series (C_1).

EXPERIMENT 2

In this study the distance between the training and the test stimuli was gradually enlarged in order to examine the effects of series shifts. According to Koffka (1935) and Johnson (1949a,b) series shifts enhance context effects in humans.

Animals. — The subjects were six chickens *(Hubbard)*, approximately seven weeks old at the beginning of the experiment. Housing conditions were the same as described in Experiment 1.

Apparatus. — The apparatus was the same as that used in Experiment 1.

Stimulus material. — Table 2 shows the three sets of training and test stimuli used (volume in ccm; log steps). Six subjects, two in each group, were trained either with middle-sized (181 and 724 ccm) or with small (45 and 181 ccm) or large (724 and 2896 ccm) cubes and tested with both ascending and descending test series. In this way, a between-group design (training) was combined with a within-group design (testing).

Procedure. — The training procedure was the same as described in Experiment 1. The test phase included generalization tests with the sets of stimuli shown in Table 2. Each test series was presented six times daily during five test days. The order in which the tests were given and the number of tests administered to each subject can be seen in Figure 3.

Results and Discussion

Figure 3 shows the obtained results using the *PSI* as an indicator of changes of the psychometric functions.

Each of the six panels of Figure 3 shows the *PSI*-values for one subject as a function of context series. Step-by-step series shifts in the ascending direction (chicken No. 15, 16, and 18) result in increasing *PSI*-values whereas series shifts in the descending direction result in decreasing values (chicken No. 17, 19, and 20). A change in the direction of shift leads to a corresponding directional shift (indicated by the roman

Table 2

Sets of training and test stimuli used for gradual series shifts

	PHYSICAL SCALE (VOLUME IN CCM)																	
	22	32	45	64	90.5	128	181	256	362	512	724	1024	1448	2048	2896	4096	5791	8000
TRAINING STIMULI							181				724							
TEST SERIES							181	256	362	512	724	1024	1448					
								256	362	512	724	1024	1448	2048				
									362	512	724	1024	1448	2048	2896			
										512	724	1024	1448	2048	2896	4096		
											724	1024	1448	2048	2896	4096	5791	
												1024	1448	2048	2896	4096	5791	8000
					90.5	128	181	256	362	512	724							
				64	90.5	128	181	256	362	512								
			45	64	90.5	128	181	256	362									
		32	45	64	90.5	128	181	256	362									
	22	32	45	64	90.5	128	181											
TRAINING STIMULI			45				181											
TEST SERIES			45	64	90.5	128	181	256	326									
				64	90.5	128	181	256	362	512								
					90.5	128	181	256	362	512	724							
						128	181	256	362	512	724	1024						
							181	256	362	512	724	1024	1448					
								256	362	512	724	1024	1448	2048				
									362	512	724	1024	1448	2048	2896			
										512	724	1024	1448	2048	2896	4096		
											724	1024	1448	2048	2896	4096	5791	
												1024	1448	2048	2896	4096	5791	8000
TRAINING STIMULI											724				2896			
TEST SERIES									362	512	724	1024	1448	2048	2896			
								256	362	512	724	1024	1448	2048				
							181	256	362	512	724	1024	1448					
						128	181	256	362	512	724	1024						
					90.5	128	181	256	362	512	724							
				64	90.5	128	181	256	362	512								
			45	64	90.5	128	181	256	362									
		32	45	64	90.5	128	181	256										
	22	32	45	64	90.5	128	181											

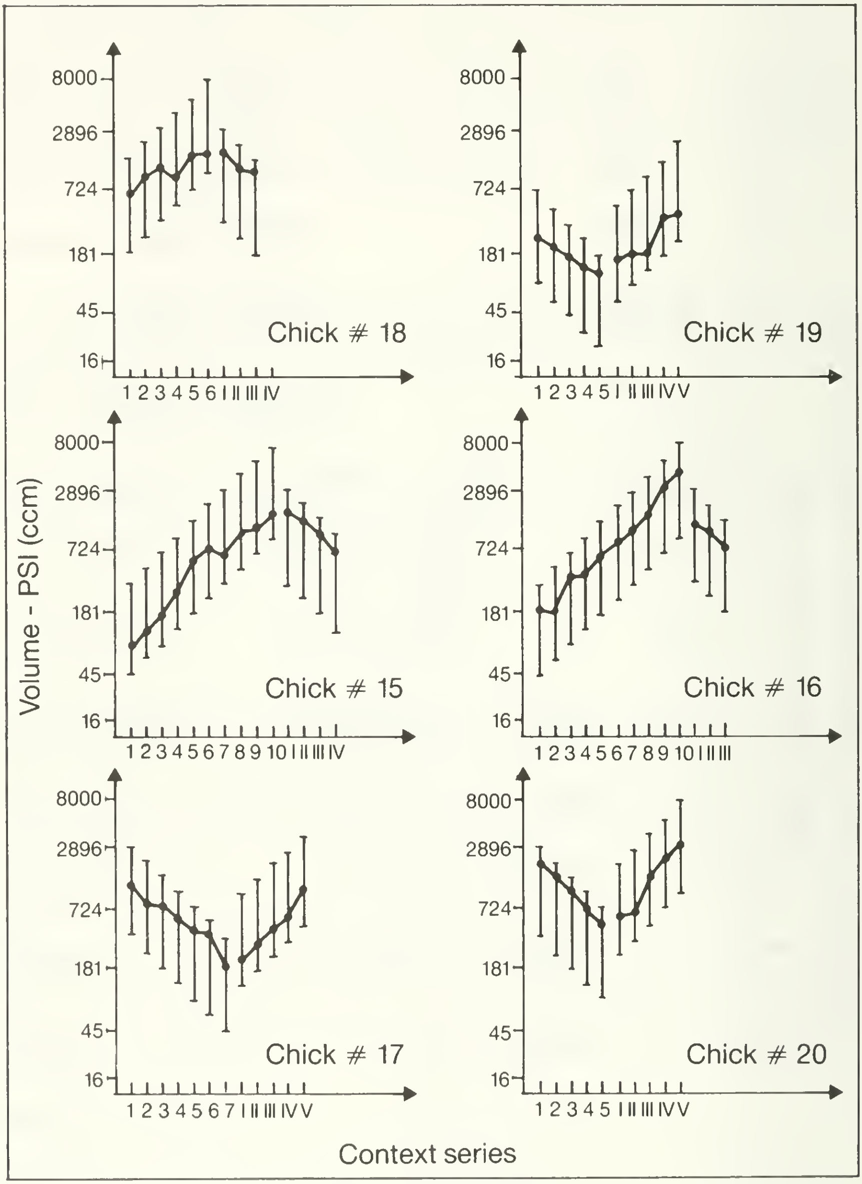


Figure 3

Changes of the Point of Subjective Indifference (PSI) over gradual context-series shifts. — *PSI* values (ordinate) increase for ascending test series and decrease for descending test series (abscissa). The arabical numbers on the abscissa indicate the direction of the first series shift for each *S*, the roman numbers the respective changes of shift direction.

numbers at the top absissa). Note that chicken No. 18 and 19 were trained with the same middle-sized TS but tested with the ascending and descending series presented in different orders. The obtained changes in the psychometric functions are very similar to those of human subjects. In addition, for both animals and humans, ascending testing again seems to produce larger contextual effects than descending testing (cf. Hauf, 1987; Johnson, 1949a,b; Zoeke & Sarris, 1987).

GENERAL DISCUSSION

The present data corroborate the prediction that contextual effects, which have previously been demonstrated only in humans, are also found in animals. At the same time, it must be taken into account that the changes in the psychometric functions found for the present subjects take place much slower than in humans. One reason for this might be the amount of training animals require to learn the discrimination task as James (1953) and Thomas (1974) have assumed. This is reflected by the empirical weighting factor k of the *FR* model that is used here. Failures to observe similar effects by prior investigators may to be understood in terms of testing techniques (continuous testing procedure) as well as in quantitative modeling of the expected effects. Therefore, an advantage of the *FR* model is that it considers the effects of both training and testing procedures (cf. Equation 1; PSI_{train}, PSI_{test}). Consideration of these matters is just a step towards a detailed quantitative model appropriate for comparison among species, and an understanding of the biopsychological processes involved in the behavior studied here.

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A COMPARISON BETWEEN AGONISTIC BEHAVIOR OF RATS OF WISTAR AND WEZOB STRAIN *(RATTUS NORVEGICUS)*

A. Nijssen and M.J. van Rijswijk

ABSTRACT: Agonistic behavior of rats of the Wistar and WEzob strain was compared. Two male rats of the same strain or two male-female pairs of the same strain were confronted with each other for a period of one hour. Individuals and pairs were unknown to each other. In the week before the pairs or the single males were placed in the two compartments of a box. By removing a separating panel, encounters could take place. Behavior was videotaped and analyzed afterwards. During the confrontation session, males from pairs displayed far more consummatory acts (clinch fights and attacks, i.e., biting or attempting to bite) than the individual housed males. The individually housed males, however, showed overall longer agonistic behavior, but this consisted of mainly appetitive agonistic behavior such as lateral attack, keeping down, keep off lying, than males from pairs. There were striking differences between strains: Wistar males from pairs showed more frequent and longer clinch fights and attacks than those of the WEzob strain. The former got far more wounds. It seems that belonging to the losing strain in interstrain encounters is not a good predictor of the amount of intrastrain aggression. The WEzob females displayed more frequent and longer appetitive behavior than the Wistar females. In male-female interactions the WEzob rats displayed more frequently some appetitive behaviors than the Wistar rats, but the Wistar rats displayed more and longer clinch fights than the WEzob rats. The enhancement of male aggression by the presence of a female seems to be a strain-dependent phenomenon.

Usually male rats display agonistic behavior against intruders in their residence, especially if this intruder is a male. This agonistic behavior of the resident male is labelled as territorial behavior, i.e., behavior to retain territory. Rats trying to extend their territory at the cost of neighbouring rats also display agonistic behavior (Calhoun, 1962; Moyer, 1971). The resident rat is usually the winner. This phenomenon is known as the prior residence or ownership effect (Waser and Wiley, 1979). If the loser cannot flee, as is common in experimental situations, a dominant-submissive relation is established. Social isolation enhances agonistic behavior of male rats (Blanchard & Blanchard, 1979) and so does the presence of a female or her odor in the cage (Flannely & Lore, 1977).

In interstrain encounters WEzob rats (a Dutch strain) are defeated by S3 rats (Tryon Maze dull rats) but win over Wistar rats (Van de

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Poll, Smeets, Van Oyen & VanderZwan, 1982). This suggests that S3 rats are more aggressive than WEzob rats and WEzob rats more than Wistar rats. This is in agreement with the statements of many investigators that Wistar rats are tame or dull animals. In the catalogue of the Dutch governmental institute for breeding laboratory animals the WEzob is characterized as aggressive. In the experiments of Van de Poll, et al. (1982), interstrain encounters between WEzob and Wistar rats were observed. Pilot studies of intrastrain encounters in Wistar rats as well as in WEzob rats showed there might be differences between intra- and interstrain agonistic behavior.

Environmental conditions are very important for the appearance of fighting and fleeing. Environmental factors can be the origin on strain differences. Rats must be housed in the experimental closure at least a couple of days to establish a territory. A simulation of a natural territory is impossible because in nature home ranges amount to several hundreds of meters in length with a width of 15 meters (Taylor, 1978). As it is known that social isolation, especially in youth, can increase aggressive behavior, the males that would be housed individually during the experiment, had to grow up in same sex male groups to make sure that the agonistic behavior of the single males could not be attributed to social isolation. A short period of isolation, one week, either does not or minimally influences that behavior (Adams, 1976; Timmermans, 1978).

The Wistar and WEzob rats were investigated under two conditions. In one condition, two individually housed male rats from the same strain were confronted with each other. In the other condition, two male-female pairs from the same strain were confronted with each other. In both conditions the rats stayed in the experimental box the week before testing. This set up presents a problem in the case of the male-female pairs. When the two male-female pairs confront each other, the males will try to copulate with the unknown female. But in the week before testing when the females were in the company of a male, they tended to be in oestrus at least once. Therefore, they were pregnant at testing if the male and female were typical. The pregnant female would then reject the males and a fight between them would arise.

Agonistic behavior has two aspects: attack and flight. Attack behaviour consists of a number of acts and postures which ultimately lead to biting the opponent. Biting and attempts to bite are the end or the goal of the whole offensive behavioral pattern and were therefore considered the consummatory acts of the offensive or attack behavior. The other acts of this pattern leading to the goal behavior were considered appetitive attacking behavior. Flight behavior, too, is divided into these two categories. Flight behavior either leads the rat to a place in which it does not meet danger, or to behavior which minimizes attacking behavior. Fleeing therefore was seen as consummatory; other non-

combative withdrawing acts were considered appetitive flight behavior (Archer, 1976).

Rats which chased away the others or were avoided were classified as winners and dominant; fleeing rats or rats which avoided other rats were classified as losers and submissive. Most probably the winners would be in control of the whole enclosure: its own chamber and that of the loser.

METHOD

Animals:. 100 rats of the *Rattus norvegicus* species (Central Institute for the breeding of Laboratory Animals, TNO, Zeist, The Netherlands) were studied. 58 were of the strain Cpb: (WU) Wistar and 42 of the strain Cpb: (WE) WEzob. Age varied from 60 to 65 days on arrival at the laboratory. The males weighed from 200 to 224 g; the females from 175 to 199 g.

Housing. The Wistar rats were housed in same sex groups of ten, the WEzob in same sex groups of seven, in macrolon cages (55x38x18 cm) (RUCO, Valkenswaard, The Netherlands) with foodpellets (Hope Farms, Woerden, The Netherlands) and water always available.

The groups from which opponents came, were housed in different air conditioned rooms, on a 12:12 reversed light/dark cycle with lights out at 0400, maintained at a temperature of 23°C, and a relative humidity of 50%. Light came from four neon bulbs on the ceiling four meters above the floor; in the dark period a red lamp was on.

Apparatus. Testing took place in a plexiglass enclave, 180x120x30 cm, covered with a wire netting, mesh width 0.5 cm. The enclosure was separated into two 90x120x30 cm chambers by a divider of plexiglass with two trap doors 15x15 cm, one 30 cm from the front wall, the other 30 cm from the back wall.

1. The floors of both chambers were covered with sawdust. In both of them there were some small bricks and a piece of wood on the floor.
2. In the left rear corner of the left chamber and in the right rear corner of the right chamber was a plexiglass sleeping box of 20x20x15 cm.
3. In the front part of both chambers, there were food pellets in the sawdust. In both chambers a waterbottle hung vertically, in the left cage from the left wall, in the right cage from the right wall.
4. A videocamera (JVC, model GS-1500), videotimer (FOR, VTG-33) and monitors (Sony) were in a room next to the testing room.

Procedure. In the middle of the dark period, a female-male pair of the same strain, or a single male of the same strain, was placed in each of the two chambers of the testing enclosure. Six days later, after 144 hours, the trap doors were opened in the middle of the dark period for one hour; videorecordings were made of the behavior of the animals. Light was provided by two red neon bulbs. The animals were selected at random from the home cages. Age varied from 90 to 165 days at the time of observation. In any test the animals were of the same age. After testing the animals were put back in their original housing conditions. Twenty female-male Wistar pairs (40 Ss) were housed pair by pair, 18 Wistar males individually, 14 WEzob pairs (28 Ss) pair by pair and 14 WEzob males individually. The coding of the registered behavior on video was independently done by two observers. In case of disagreement about the coding of a behavioral element it was analyzed again until there was agreement between the observers. Time was registered by means of the videotimer. For each experimental condition the frequency of each behavioral element was determined in addition to the duration in seconds of each clinch fight. The total duration of agonistic behavior per experimental condition was estimated by means of a combination of time and event sampling. Every period of ten seconds of the whole hour videoregistration was screened if the interval contained offensive or defensive acts. The number of intervals with such acts x ten seconds was used as the estimation of the duration of agonistic acts.

Behavior coding. 22 elements of behavior, based on the scheme of Timmermans (1978) were distinguished as follows: (see Figure 1)

1. Lateral posture, aa. The rat shows an arched back, one of its flanks is directed to the head of the opponent. The head and the muzzle are in a wry position, bent to the floor and directed towards the opponent. Sometimes one or both forelegs, and sometimes a hindleg, are off the floor.
2. Lateral attack, aa. From a lateral posture the rat pushes, punches and kicks the opponent.
3. Keeping down, aa. The rat bends over the opponent and presses the opponent against the floor with one or both forelegs on the trunk and/or head of the opponent.
4. Social grooming, m. The rat licks and combs the fur of the opponent, often combined with keeping down. The opponent is standing, lying or sitting.
5. Crawling underneath, m. The rat passes under the head, or wriggles under the trunk of the opponent, which often stands half upright. The movement occurs from a frontal or lateral position.
6. Following, aa. The rats walks or runs after the opponent which moves away.

7. Mounting, m. The mounting rat puts its forelegs on the back and the flanks of the opponent, pressing chest and head against the mountee.
8. Kicking backwards, fa. The standing or waking rat, straight before the opponent, kicks with hindlegs if the opponent approaches too closely, follows or mounts.
9. Leaping up, aa. From an upright posture two rats leap up perpendicularly with stretched forelegs, or one of the two leaps up, with the other in a different posture.
10. Lying/crawling, m. The rat, broad backed, lies with its abdomen pressed against the floor. The rat crawls with sliding genitals.
11. Marking, m. The rat rubs an object with abdomen and/or genitals.
12. Keep-off lying, fa. The rat lies on its back and moves its legs in the direction of the opponent.
13. Keep-off sitting, fa. The rat raises its forelegs, genitals and the part of the abdomen close to the genitals remain on the floor. The rat may be pressed to the wall of the cage. The forelegs move in the direction of the opponent.
14. Half upright parry, fa. The rat in half upright posture moves and eventually pushes in the direction of the opponent.
15. Boxing, fa. The rats stand upright and move their forelegs in the direction of the opponent.
16. Standing upright, fa. Both rats stand motionless on their hind legs against each other with forelegs and sometimes noses touching each other.
17. Half upright, fa. The rat stands with an arched back and with forelegs lifted; it is directed to the opponent.
18. Pushing, fa. The standing or lying rat pushes with its head, forelegs or trunk the opponent from its spot.
19. Tail rattling, m. The rat makes a horiziontal undulating movement with its tail; across the floor.
20. Fleeing, fc. The rat runs away fast from the standing or following opponent.
21. Attack, ac. The rat's head moves fast toward the opponent in an attempt to bite it (not followed by clinch fight).
22. Clinch fight, ac. The rats roll over the floor together while they try to bite each other; often one gets bitten.

STATISTICS

For the male-male encounters an Anova with strains and conditions as factors was executed for each behavioral element and for the total duration of the agonistic behavior. A total of 23 Anova's were executed.

FIGURE 1

Categorization of the behavioral elements

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attack
- appetitive: 1, 2, 3, 6, 9 (aa)
- consummatory: 21, 22 (ac)

flight
- appetitive: 8, 12, 13, 14, 15, 16, 17, 18 (fa)
- consummatory: 20 (fc)

The elements 4, 5, 7, 10, 11 and 19 appear in agonistic situations, but are difficult to categorize as attack or flight and so they were classified in the category "miscellaneous" (m).

As the same data were used for many statistical tests the chance to make a type I error is larger than the planned level of significance. Therefore each Annova was compared with a multivariate significance level of alpha/n, where n is the total number of the Anova's (Miller, 1966). In this case the significance level is .05.23 = .0022.

As a second step in preventing unwarranted conclusions, multiple comparisions were made with the Fisher LSD or protected t test. This t test makes use of the MS_w of the Anova's (Welkowitz, Ewon & Cohen, 1976; Hays, 1963; Winer, 1962). The same procedure was used for the testing of the female-female and the male-female encounters, with only the strain as a factor.

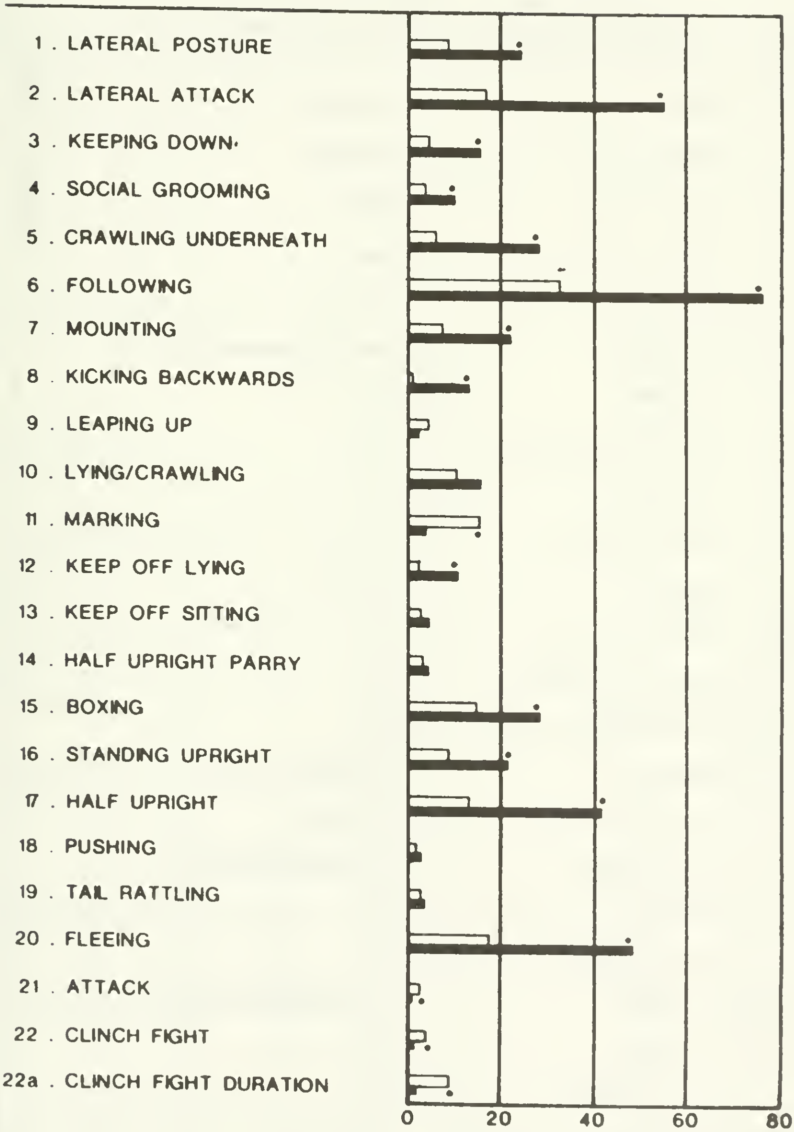
RESULTS

After opening the trap doors, generally, the rats first explored the enclosure of their opponents, then within five minutes they made body contact, sniffing muzzles and genitals. As the animals had been neighbors for 144 hours before the meeting they probably knew the sounds and odor of each other.

1. *Male-male encounters.* Six of the 23 Anova tests with conditions and strains as factors were significant at the .0022 level. So there was a difference between males from pairs and single males, main effect, and between Wistar and WEzob rats, main effect (Figure 2 and 3).

FIGURE 2

Males From Pairs Versus Single Males: Both Strains Combined (Main Effect)[**]



Mean frequencies of behavioral elements and mean duration of clinch fights in seconds. White bars = males from pairs: black bars = single males.

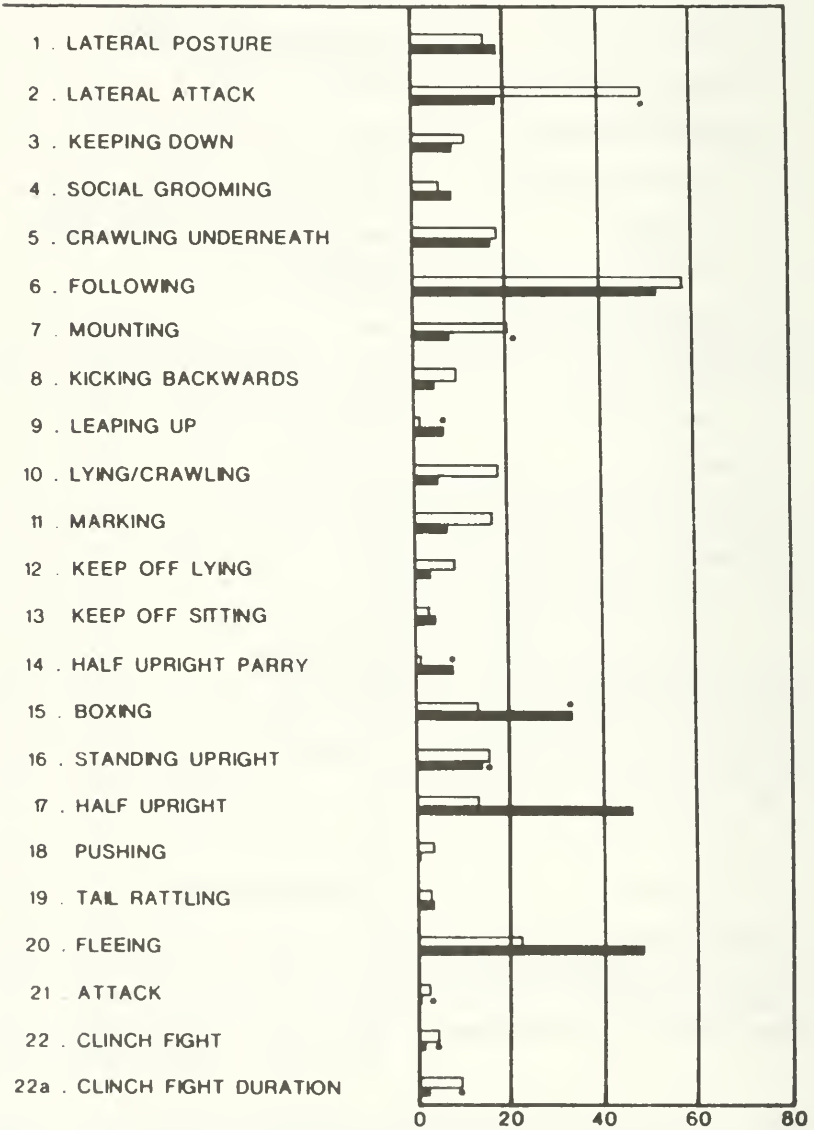
[**]$p < .05$: ANOVA F TEST

[*]$p < .05$, multiple comparisons

FIGURE 3

*Wistar Versus WEzob Males: Both Single and Paired Males Combined (Main Effect)***

Mean Frequencies of Behavioral Elements and Mean Duration of Clinch Fights in Seconds



White bars = Wistar Males: black bars = WEzob males.
**$p < .05$: ANOVA F Test
*$p < .05$, multiple comparisons

Computation of the t-values according to Fisher LSD procedures made clear which variables account for the differences (Table 1).

TABLE 1

Male-male encounters: Fisher LSD t test of every ANOVA F test significant at .05 level.
wip = Wistar males from pairs; wis = Wistar single males; wep = WEzob males from pairs; wes = WEzob single males.
aa = attack appetitive; ac = attack consummatory; fa = flight appetitive; fc = flight consummatory.

Behavioral element	Intragroup & Interstrain	Fisher LSD t	p
1. Lateral posture - aa	wip-wis	- 1.71	.10
	wep<wes	- 2.02	.05
2. Lateral attack - aa	wip<wis	- 3.41	≤ .001
	wep-wes	- .45	.66
	wip-wep	.28	.78
	wis>wes	2.97	.01
3. Keeping down - aa	wip<wis	- 2.53	.02
	wep-wes	- .93	.36
4. Social grooming - m	wip<wis	- 2.4	.02
	wep-wes	- .93	.36
5. Crawling underneath - m	wip<wis	- 3.12	.006
	wep<wes	- 2.72	.02
6. Following - aa	wip<wis	-30.8	≤.001
	wep<wes	-27.7	≤.001
7. Mounting - m	wip<wis	- 3.44	≤.001
	wep-wes	- .40	.69
	wip-wep	.10	.85
	wis>wes	2.97	.01
8. Kicking backwards - fa	wip<wis	- 3.29	≤.001
	wep-wes	- 1.21	.24
9. Leaping up - aa	wip<wep	- 4.29	≤.001
	wis<wes	- 2.62	.01
10. Lying/crawling - m	wip>wep	2.4	.02
	wis<wes	- 1.44	.16
11. Marking - m	wip>wis	3.86	≤.001
	wep-wes	.02	.98
	wip>wep	4.67	≤.001
	wis-wes	1.18	.25

TABLE 1 *(cont.)*

Behavioral element	Intragroup & Interstrain	Fisher LSD t	p
12. Keep off lying - fa	wip<wis	- 2.8	.01
	wep-wes	- .8	.43
14. Half upright parry - fa	wip<wep	- 3.39	≤.001
	wis<wes	- 3.47	≤.001
15. Boxing - fa	wip<wis	- 2.18	.04
	wep-wes	- 1.00	.33
	wip<wep	- 2.8	.01
	wis-wes	- 1.96	.06
16. Standing upright - fa	wip<wis	- 2.44	.02
	wep-wes	- 1.46	.15
17. Half upright - fa	wip-wis	- .8	.43
	wep<wes	- 4.89	≤.001
	wip-wep	- .8	.43
	wis<wes	- 5.4	≤.001
18. Pushing - fa	wip-wep	1.10	.28
	wis>wes	2.28	.03
19. Tail rattling - m	wip<wis	- 2.4	.02
	wep-wes	- 1.44	.16
20. Fleeing - fc	wip-wis	- .80	.43
	wep<wes	- 3.50	≤.001
	wip-wep	- .19	.85
	wis<wes	- 3.24	≤.001
21. Attack - ac	wip>wis	3.34	≤.001
	wep-wes	- .16	.87
	wip>wep	3.96	≤.001
	wis-wes	.78	.44
22. Clinch fight - ac	wip>wis	3.6	≤.001
	wep-wes	.46	.65
	wip>wep	3.24	≤.001
	wis-wes	.17	.87
22a. Clinch fight duration	wip>wis	4.17	≤.001
	wep-wes	.06	.95
	wip>wep	3.9	≤.001
	wis-wes	.18	.86
Cumulative duration agonistic behavior	wip<wis	2.78	.013
	wep<wes	4.06	.002

Interaction effects were not significant at the .0022 level.

1.1 Conditions.

a. Wistar males from male-female pairs showed more marking (m), attack (ac), clinch fights (ac) than single males and the duration of clinch fights of males from pairs was longer than that of single males. Single Wistar males showed more lateral attack (aa), keeping down (aa), social grooming (m), crawling underneath (m), following (aa), mounting (m), kicking backwards (fa), keep off lying (fa), boxing (fa), standing upright (fa), tail rattling (m), than Wistar males from pairs.
b. Single WEzob males showed more lateral posture (aa), crawling underneath (m), following (aa), half upright (fa) and fleeing (fc) than the WEzob males from pairs.
c. The cumulative duration of agonistic behavior of single Wistar and WEzob males was longer than that of Wistar and WEzob males from pairs.
d. Besides this, 16 of the 18 Wistar males from pairs had at least one but usually more wounds; none of the Wistar males had a wound. Of the 14 WEzob males from pairs only one animal had a wound; none of the single males had one.

1.2 Strains.

a. Comparison between males from pairs. Wistar males showed more lying/crawling (m), marking (m), attack (ac), clinch flight (ac) than WEzob males. The duration of clinch fights and the overall duration of agonistic behavior were longer in Wistar than in WEzob males. WEzob males showed more leaping up (aa), half upright parry (fa) and boxing than Wistar males.
b. Comparisons between singles. Wistar males showed more lateral attack (aa), mounting (m) and pushing (fa) than the WEzob males. WEzob males showed more leaping up (ac), half upright parry (fa), half upright (fa) and fleeing (fc) than Wistar males.
c. Most Wistar rats had several wounds and blood on their fur; only one WEzob rat had a wound.

1.3. Winners and losers.

a. Wistar pair condition. Winners could be easily distinguished from losers. Losers fled to the platform of the sleeping box and if they came down they were chased back by the winners. Winners showed more lateral attack (aa), following (aa), lying/crawling (m), crawling underneath (m) and attacks than losers ($p < .05$); losers displayed

more half upright parry (fa) and fleeing (fc) than winners did ($p < .05$).

b. WEzob pairs condition. In the WEzob groups it was more difficult to distinguish winners from losers. However, one male always showed a greater tendency to flee than the other. The latter was considered to be the winner, the former the loser. It turned out that in WEzob pair condition winners displayed more lateral posture (aa) and lateral attack (aa; for both $p < .0179$) than losers.

c. The single condition. In the WEzob single condition the winner showed more lateral posture (aa), lateral attack (aa), following (aa), lying/crawling (m) and crawling underneath (m) ($p < .02$) than the loser. In the Wistar single condition the winner showed more lateral attack (aa) than the loser ($p = .023$).

2. Female-female encounters.

Three of the 23 Anova tests with strains as a factor were significant at the .0022 level. So there is a significant difference between the Wistar and WEzob female rats (Figure 4).

Calculation of Fisher's LSD t-values (table 2) leads to the conclusion that WEzob females showed more lateral attack (aa), keeping down (aa), crawling underneath (m), following (aa), mounting (m), kicking backwards (fa), keep off sitting (fa), half upright parry (fa), half upright (fa), fleeing (fc) than the Wistar females.

The accumulative duration of agonistic behavior of WEzob females was longer than that of the Wistar females.

3. Male-female encounters.

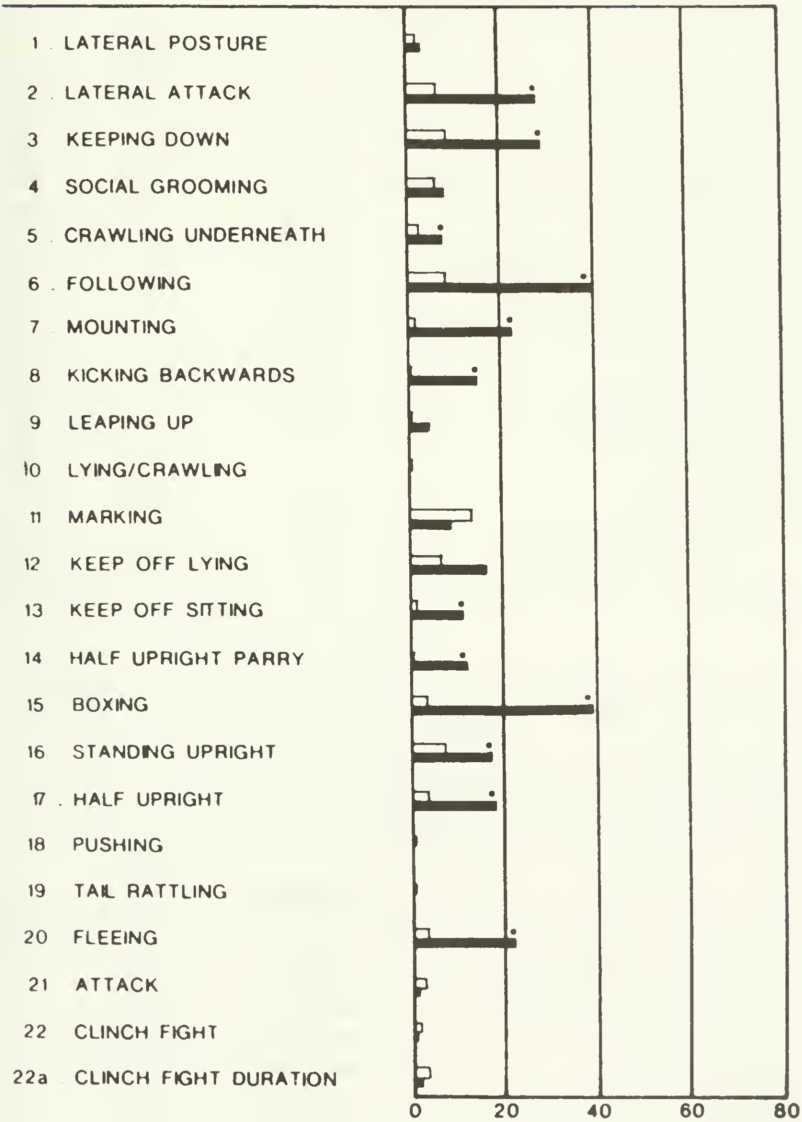
The behavioral elements of both sexes builded up the score of the interactions. So the total frequencies or durations of a behavioral item for the male-female pair, rather than for individual animals, were analyzed. Two of the Anova's with strains as a factor were significant at the .0022 level. There is a difference between Wistar and WEzob male-female interactions (Figure 5).

The results of the Fisher LSD procedure (table 3) lead to the conclusion that in WEzob male-female interactions there is more crawling underneath (m), kicking backward (fa) half upright parry (fa), boxing (fa), half upright (fa) than in Wistar male-female interactions.

In Wistar male-female interactions there is more pushing (fa), clinch fight (aa) and the duration of clinch fight is longer than in WEzob male-female interaction. The cumulative duration of agonistic behavior of the WEzob male-female interactions was longer than the Wistar male-female interactions.

FIGURE 4

Wistar Versus WEzob Females: Mean Frequencies of Behavioral Elements and Mean Duration of Clinch Fights in Seconds



White Bars = Wistar Females: Black Bars = WEzob Females: *p ≤ .05, multiple comparisons

TABLE 2

Female-female encounters: Fisher LSD t test of every ANOVA F test significant at .05 level.

aa = attack appetitive; ac = attack consummatory; fa = flight appetitive; fc = flight consummatory

Behavioral element	Interstrain	Fisher LSD t	p
2. Lateral attack - aa	we<wi	-2.47	.03
3. Keeping down - aa	we>wi	-2.6	.02
5. Crawling underneath - m	we>wi	-2.78	.01
6. Following - aa	we>wi	-3.26	.01
8. Kicking Backwards - fa	we>wi	-4.72	≤.001
7. Mounting - m	we>wi	-4.2	.001
13. Keep off sitting - fa	we>wi	-3.37	.005
14. Half upright parry - fa	we>wi	-3.47	.004
15. Boxing - fa	we>wi	-4.48	.001
16. Standing upright - fa	we>wi	-2.20	.05
17. Half upright - fa	we>wi	-2.98	.01
19. Tailrattling - m		.265	.75
20. Fleeing - fc	we>wi	-2.96	.01
Cumulative duration agonistic behavior	we>wi	-4.767	.001

TABLE 3

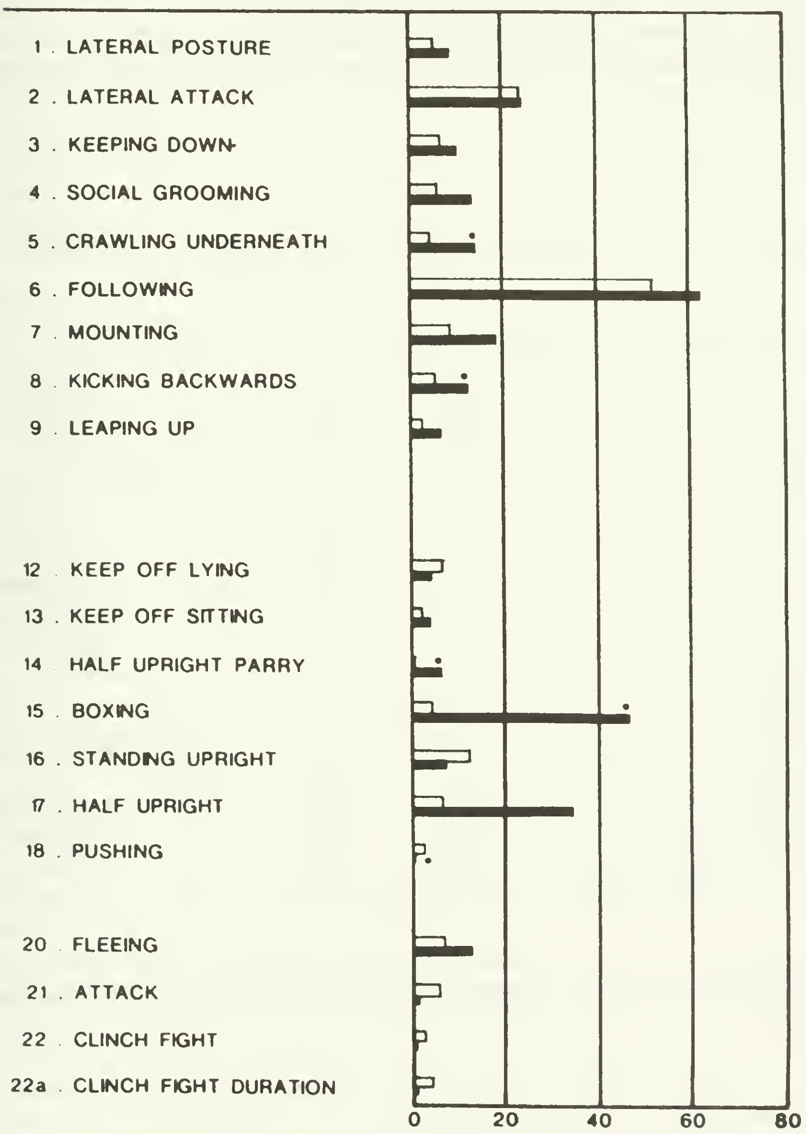
Male-female encounters: Fisher LSD t test of every ANOVA F test significant at .05 level.

aa = attack appetitive; ac = attack consummatory; fa = flight appetitive; fc = flight consummatory

Behavioral element	Interstrain	Fisher LSD t	p
5. Crawling underneath - m	we>wi	-2.95	.01
8. Kicking backwards - fa	we>wi	-2.6	.02
14. Half upright parry - fa	we>wi	-6.76	.001
15. Boxing - fa	we>wi	-2.88	.01
17. Half upright - fa	we>wi	-4.46	.001
18. Pushing - fa	wi>we	2.19	.05
22. Clinch fight - ac	wi>we	2.42	.03
22a. Clinch fight duration	wi>we	2.38	.03
Cumulative duration agonistic behavior	we>wi	-2.97	.01

FIGURE 5

Wistar versus WEzob Male-Female Interactions: Mean Frequencies of Behavioral Elements and Mean Duration of Clinch Fights in Seconds: Fisher LSDT test.



White Bars = Wistar Male-Female Interactions:
Black Bars = WEzob Male-Female Interactions: *p ≤ .05, multiple comparisons

4. Further explorations

There were some differences between males and females from the male-female pairs in their interactions (table 4). a. Wistar males showed more keeping down (aa), following (aa), mounting (m) than Wistar females. Wistar females showed more kicking backwards (fa) than Wistar males. b. WEzob males showed more following (aa), mounting (m) than the WEzob females; the latter showed more lateral attack (aa) and kicking backwards (fa).

TABLE 4

Differences between males and females of the male-female interaction.
Anova, F test, $p < .05$, two-tailed.

wim = Wistar male; wif = Wistar female; wem = Wistar male; wef WEzob female.

Behavioral element	Mean frequency Male	Female	p-value	Male vs Female
Wistar				
2. Lateral attack - aa	3.67	20.44	.0256	—
3. Keeping down - aa	6.22	1	.011	wim>wif
6. Following - aa	38.44	14.89	.006	wim>wif
7. Mounting - m	8.78	0	.005	wim>wif
8. Kicking backwards - fa	.11	6.71	.012	wim<wif
Wezob				
2. Lateral attack - aa	3.86	20.71	.012	wem<wef
3. Keeping down - aa	8.57	3.43	.102	—
6. Following - aa	42.29	20.14	.017	wem>wef
7. Mounting - m	15.86	2.86	.018	wem>wef
8. Kicking backwards - fa	1.14	11.43	.011	wem<wef

Although there were different behavioral patterns for males and females, at the .05 level of probability a firm conclusion is not warranted.

DISCUSSION AND CONCLUSIONS

The most striking outcome is that the Wistar males in the presence of females showed more vehement attacking behavior than the WEzob

males in the same conditions and than the single males of either of the two strains. They showed the highest frequency of attack and clinch fights, the cumulative duration of the latter was longer than in any other group. Besides that they had by far the most wounds and they had clearly perceptible blood on their fur. As the single Wistar male also showed more aggression than the single WEzob male this might mean that belonging to the losing strain in interstrain encounters is not a good predictor of the amount of intrastrain aggression. The second surprise was that the presence of females had only an influence on the behavior of males in the Wistar strain. So the influence of the female presence on male aggressive behavior seems to be strain-dependent and prominent in the Wistar strain, a strain that showed already more attack behavior.

Single males of both Wistar and WEzob strain showed a greater variety of agonistic behavior than males in the company of females. The cumulative duration of their agonistic behavior was longer too. Maybe the activation of their agonistic system was high enough to release various elements of appetitive behavior, but not high enough to release consummatory acts such as biting and clinch fighting.

A clearly dominant and submissive relationship could only be spotted among the Wistar males in company of females: After the fighting took place the loser fled to a safe spot. It seems plausible to assume that there is a relation between the high attack level and the accompanying wounds of these male Wistars and the establishment of a definite dominance-submission relationship. In the other conditions only the number of flights distinguished winners from losers.

In females no dominance and submissive relationship was found. Three hours after the beginning of their meeting, when the light period started, several females even slept together in the sleeping boxes. There were some differences between WEzob and Wistar females. The former showed a higher frequency of 12 out of the 22 behavioral elements, but this did not lead to a dominance and submission relationship.

Agonistic interactions between females and males occurred on two occasions: 1) either when the males tried to mount the females (all pregnant and all had a litter approximately two and half weeks later) who reacted by kicking backwards and after that with lateral attack: 2) or when two males in their joint agonistic interactions bumped on a female and continued their agonistic behavior but now with her as a target until they noticed their mistake. Females display agonistic behavior only after undesired body contacts. So, it appears that in both strains the competition for territory is between males. Wistar rats are more attack prone than WEzob in intrastrain encounters. Only the female Wistar stimulates a high "vehemence" in the already more aggressive male of her strain.

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SEQUENTIAL PATTERNS OF BEHAVIOR IN THE BLACK BUCK, *ANTILOPE CERVICAPRA* (LINNAEUS)

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ABSTRACT: Six male and six female black bucks were observed in the Trivandrum Zoo for one year. Sequential patterns of behavior were homogeneous throughout all observation periods. Sequences were longer with more acts occurring during morning hours than evening hours. However, acts were of shorter duration during noon hours. Sexually dimorphic features were reflected in the behavior sequences. The dominant buck was more active and aggressive than other group members. The behavior sequences of the black bucks are explained in terms of a first order Markov chain with five states. Inhibiting and directing behavior patterns are discussed within an ecological, functional framework.

INTRODUCTION

A sequential pattern of behavior is an ordered succession of identified behavioral activities of an animal at any time period. The behavioral sequence of an animal at any time is set up on the basis of various internal and external factors (Baerends, 1985). Investigations of sequential patterns of behavior have considerable relevance in formulating behavioral models and in the prediction of future states of behavior of any animal species.

Various activities of animals do not occur at random, but fall into a homogeneous pattern of sequence (Hinde & Stevenson, 1969). This integration of heterogeneous units into a sequence depends on a variety of factors operating at different levels. McFarland (1969) described how a sequence of behavioral transitions occur by the 'inhibition, disinhibition and reinhibition' processes. A dominant state of behavior permits a disinhibited behavior to appear for a certain time period showing the 'time-sharing' phenomenon.

Chase (1974; 1980; 1982a; 1982b; 1985) developed new theoretical and methodological approaches to the study of sequential analysis of behavior in a few species of animals. However, data on mammals necessary for ethological theory are scanty (Bekoff, 1977; Seyfarth, Cheney & Hinde, 1978) and hence the present investigation studies and analyses the sequential pattern of behavior of the Black Buck, *Antilope cervicapra*.

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METHODS

Animals: Black bucks were kept in an open enclosure at the Trivandrum Zoo. In August, 1985, during the initial period of this investigation, this group consisted of 24 females, 21 males, and four fawns. For the present investigation, six male and six female adults were selected at random. These individuals were identified on the basis of their dominance status, determined during the preliminary observation period (see below), the nature of horns, body color and other identification marks seen on different parts of their body. They were designated as M1, M2, M3, M4, M5 and M6 (males) and as F1, F2, F3, F4, F5 and F6 (females).

PROCEDURES

On the basis of the two-week preliminary observation, various observable behaviors of the black buck were identified. These behavioral activities were categorised into the following five states on the basis of functional features.

State 1. Behavior in relation to olfaction
State 2. Feeding behavior
State 3. Behavior in relation to aggression
State 4. Grooming and licking
State 5. Reproductive behavior

Direct behavioral observations were made for a period of one year from August, 1985 to July, 1986. Only one animal was observed at a time. Each observation period was two hours. Daily observations were made during 08 00h to 17 00h at random. Data were recorded on an observation chart and analysed by a computer to identify a first order Markov Chain in the sequential pattern of behavior.

Markov Chain analyses: Observations were made on continuous actions to estimate the transition probability matrix as detailed by Basawa and Rao (1982). 'N' transitions (i.e. 'N' sequential acts) of animals performing diverse actions belonging to the five identified states were observed. The data on individual males and females were then subjected separately for analysis using procedures for testing homogenity of behavior among females and males (Bhat, 1972). This provided concurrence for continuing the analysis by combining the observation on all animals of both sexes separately for each 2h observation period from 08 00 to 17 00h. It may be noted that the transition matrix explains the Markov Chain.

The estimated Markov Chain model for the sequential dependence in behavior was subjected to a contingency test for inference purpose.

A further analysis for identifying the specific states that account for temporal dependence was carried out, by breaking down the transition table which was found to be statistically valid (Bishop, Fienbory & Holland, 1975).

The probability matrix of order 5 was estimated for females and males separately for five time periods as given in Table 1.

TABLE 1

Estimated Transition Probabilities from Each Preceding Act to Following Act of Black Bucks (A. cervicapra)
for Five Different Time Periods

Time periods (h)	Observed states	Males 1	Males 2	Males 3	Males 4	Males 5	Females 1	Females 2	Females 3	Females 4	Females 5
0800–1000	1	.440	.075	.054	.140	.292	.428	.077	.0	.181	.313
	2	.361	.157	.108	.108	.265	.310	.169	.0	.225	.296
	3	.337	.048	.193	.157	.265	.0	.0	.0	.500	.500
	4	.421	.086	.086	.114	.293	.490	.006	.006	.116	.320
	5	.416	.058	.066	.113	.346	.473	.003	.003	.165	.299
1000–1200	1	.416	.117	.070	.117	.280	.401	.092	.003	.155	.350
	2	.427	.115	.135	.146	.177	.392	.108	.0	.176	.324
	3	.326	.109	.207	.076	.283	.0	.0	.0	.0	.0
	4	.552	.048	.057	.057	.286	.443	.078	.0	.104	.374
	5	.427	.073	.070	.089	.341	.424	.098	.0	.148	.329
1200–1400	1	.392	.121	.049	.127	.310	.397	.140	.003	.162	.301
	2	.325	.130	.142	.130	.273	.286	.186	.0	.171	.357
	3	.226	.075	.151	.075	.471	.0	.0	.0	.0	.0
	4	.422	.084	.024	.120	.349	.438	.125	.0	.086	.350
	5	.409	.077	.069	.112	.332	.452	.096	.0	.128	.324
1400–1600	1	.410	.114	.066	.116	.299	.381	.096	.0	.192	.332
	2	.319	.143	.132	.198	.209	.431	.097	.0	.194	.278
	3	.316	.066	.145	.105	.368	.0	.0	.0	.0	.0
	4	.442	.050	.058	.108	.342	.397	.074	.0	.184	.346
	5	.471	.075	.051	.156	.247	.473	.090	.0	.184	.253
1600–1700	1	.392	.091	.072	.091	.354	.447	.096	.0	.128	.329
	2	.292	.083	.167	.167	.292	.351	.108	.0	.162	.378
	3	.299	.029	.239	.119	.313	.303	.0	.0	.0	.0
	4	.228	.044	.074	.162	.500	.317	.067	.0	.2	.417
	5	.433	.055	.080	.092	.340	.438	.071	.0	.130	.361

State 1. Behavior in relation to olfaction
State 2. Feeding behavior
State 3. Behavior in relation to aggression
State 4. Grooming and licking
State 5. Reproductive behavior

To estimate the matrix, it was necessary for the chain to be homogeneous in time. This was also necessary for the practical side of observation. When treating the number of transitions of all females and males together for each state, the results showed evidence towards the homogeneity of behavior (Table 2). Homogeneity was observed in the behavior of all animals during all the observation periods. The combined χ^2 values have been given separately for males and females in Table 3. The analysed data revealed that the sequential behavior of the black bucks could be explained by a first order Markov Chain with five states. In the case of females, the hypothesis of first order Markov Chain could be accepted for the period from 0800 to 1000 h and 1600 to 1700 h only, whereas in the case of males, it could be accepted for the whole observation period from 0800 - 1700 h.

TABLE 2

χ^2 Values for Testing Homogeneity of Behavior of Black Bucks.

		Time in hours				
Sex	States of Behavior	0800-1000	1000-1200	1200-1400	1400-1600	1600-1700
Males	1	18.32	20.24	24.38	13.86	6.57
	2	6.76	7.46	30.13	16.8	17.69
	3	22.37	17.25	25.04	11.31	14.38
	4	15.01	15.91	17.58	17.46	10.29
	5	23.21	15.81	24.44	14.38	10.36
Females	1	7.77	12.41	9.49	12.98	2.46
	2	6.29	15.10	7.51	8.48	8.98
	4	15.01	13.51	18.92	19.21	15.12
	5	10.66	6.59	8.17	16.22	4.33

χ^2 20 df = 31.41 (males)
χ^2 15 df = 23 (females)
States 1-5 as in Table 1.

TABLE 3

Calculated Values of χ^2 for Testing the First Order Markov Chain.

	Time in hours				
Animals	0800-1000	1000-1200	1200-1400	1400-1600	1600-1700
Male	37.16*	48.15*	28.81*	39.59*	42.16*
Female	23.56*	8.85	12.79	8.42	36.01*

* p = .05
** p = .10

RESULTS

The observed behavioral transition and estimate of the transition probabilities revealed that the pattern of transition for an animal over different observation periods was different. However, approximately the same pattern was observed for different individuals in the same observation period. It was further revealed that state 3 (behavior in

TABLE 4

*The Relationship of Each State of Behavior in the Sequential Pattern Formation in the Black Buck**

		Directing states		Inhibiting states	
Time (h)	States°	Males	Females	Males	Females*
	1	1,4	4	3,5	1
	2	1,2,3	2,4	4,5	1
0800-1000	3	3	—	1,2,4,5	—
	4	2,3	5	4,5	1,2,4
	5	5	1	2,3,4	2,5
	1	2,4	4	1,3,5	1
	2	2,3,4	2	5	1,4,5
1000-1200	3	2,3	—	1,4	—
	4	1	1,5	2,3,4	2,4
	5	5	2	2,3,4	5
	1	1,2,4	2,4	3,5	5
	2	2,3,4	2,4,5	1,5	1
1200-1400	3	3,5	—	1,2,4	—
	4	1,4,5	1,5	2,3	4
	5	1	1	2,4	2,4
	1	2,5	2,5	1,3,4	1
	2	2,3,4	—	1,5	5
1400-1600	3	3	—	1,2,4,5	—
	4	1,5	5	2,3,4	1,2
	5	1,5	1	2,3,5	5
	1	1,2	1,2	3,4	4,5
	2	2,3,4	2,4	1,5	1
1600-1700	3	3,4	—	1,2,5	—
	4	4,5	4,5	1,2,3	1,2
	5	1	1	2,3,4,5	2,4

* State 3 was not pronounced among females
° States 1-5 as in Table 1.

relation to aggression was not important for the females of the species as there were very few transitions, showing a difference in the behavioral patterns of states with respect to transitions in the states of activities.

Even though all the behaviors were observed throughout the day, the behavioral sequences were of longer duration with more behavioral acts, during morning and evening hours. The sequences hence, were shorter, with fewer behavioral acts, during noon hours. The appearance and disappearance of behavioral phases were in relation to the time of the day.

The sequential pattern of behavior varied according to the sex and dominance status of the individuals. Females spent much of the time in roaming, eating, and resting, while the males very often indulged in several types of aggressive behaviors such as chasing, thrashing and sparring. Variation in the pattern of behavior was also observed in the sub-dominant and dominant animals. The dominant individual was found to be highly active and aggressive.

Discrimination of behavioral states as 'direction' and 'inhibition' are shown in Table 4. By observation of the data in Table 4, each of the states 1, 2, 3, 4 and 5 may be seen to direct and/or inhibit other states, as shown in Table 5.

TABLE 5

The Trends of Directing and Inhibiting Acts of the Five States of Behaviors of the Black Buck.

Sex	States°	Directing Act	Inhibiting Act
Males	1	1,2,4	3,5
	2	2,3	5
	3	3	1,2,4,5
	4	5	4
	5	1	2,3,4
Females*	1	2,4	1,5
	2	2,4	1,5
	4	5	1,2,4
	5	1	2,4,5

° States 1-5 as in Table 1.

* State 3 was not pronounced among females

DISCUSSION

A Markov Chain can be used to denote a sequence of events with the probability of future events depending on past events. A first order Markov Chain model for the sequential behavior of the black buck assumes

that the probability of an act depends on the immediately preceding act only. A Markov Chain would be characterised by the initial distribution and the transition probability matrix. For practical purposes, the initial distribution could be omitted as it corresponds to the probability that the animal was in one of these five states at birth. Since these animals have lived for a number of years, the process may have started long before the study and the initial distribution may be of no consequence.

All animals possess a behavioral repertoire during various social interactions. It would be interesting to examine the relationship among these different acts which consist of one type of act being preceded or followed by another type. For example, 'push' always precedes 'shove' (Fagen & Young, 1978). Behavioral acts of directing and inhibiting tendencies of the states of behavior at any time period can be substantiated on biological bases.

Since various types of olfactory responses of the black bucks were studied and grouped as a single state, it is possible that during olfactory signalling the animals may use various modes of signalling so as to achieve the maximum benefits. Signalling would be more effective if various modes are used even to convey the same message or to convey different messages during the same type of interactions (Mykytowycz, 1970). To some extent, grooming and licking also have the effect of chemical signalling. It may also be possible that this behavior has an inhibitory effect on aggressive tendencies during social interactions as olfactory signals would be used to convey messages of individual status. Among artiodactyles, behavior in relation to olfaction includes scent marking and related acts (Müller-Schwarze, 1983). Since most of the marking was performed by the most dominant individual of the group, others would withdraw from aggressive encounters as it would be easy for them to identify the individual and its status at any particular time. Since they are more responsible to olfactory cues of specific signals at any time, they may be less interested in other behavioral activities, unless induced by some other motives.

Feeding is one of the primary requirements of any animal species. However, in natural habitats, the animal may have to forage and seek out its food. Various behavioral interactions in relation to feeding in natural habitats are exploratory activities, locating the prey or food, responses oriented towards the food, manipulation of the food, and the feeding itself. However, in captive zoo conditions, they are acclimated to the specific feeding time and the daily availability of their ration. There may be considerable limitations in the availability of food items and each individual of the group is prompted to achieve the maximum food within the limited time. In such circumstances, a tendency is developed to go on feeding until satiation is achieved or until the maximum available food is consumed. Hence, feeding in zoo conditions will direct feeding to the maximum level. Since competition for food is very common among the individuals in such conditions, fighting is

very pronounced, especially among species which maintain a social hierarchy. This may not influence the feeding of females in the group to a significant level as fighting is not pronounced among them. Females of the black buck do not maintain a dominance hierarchy.

During aggressive encounters, the dominant male chases the sub-dominants as it has to fight to maintain control over other individuals in the group. Aggression, once it is started, can cease only on the final achievement of the goal or when the aggressive individuals with heavy injuries are isolated. Since other behaviors are interrupted on such occasions, aggression inhibits other states of activities.

Grooming and licking are considered to have prominant roles in communication signalling, in thermoregulation, in getting rid of ectoparasites and or in maintaining social cohesion among individuals of the group. It is also part of reproductive behavior as a prelude to mating behavior. Hence, grooming and licking have relevance in influencing other behavioral activities of the same or other individuals of the group. It inhibits grooming and licking by other animals because it may more often influence the reproductive behavior itself.

Since reproductive and related activities direct olfaction and related behavior, it can be confirmed that in this species olfaction has a significant role to play in the reproductive behavior. Other activities such as behavior in relation to feeding, aggression, grooming and licking are inhibited when mating and related activities progressed. Meier *et al.* (1973) and Dubost & Feer (1981) have described behavioral display during courtship in the black buck.

During noon time the behavioral sequences consisted of activities with a low threshold requiring a lower level of motivational factors or a weeker eliciting stimulus than occurring in the morning and evening hours. This factor was described as non-stationary behavior in probability, i.e., the behavior depends upon the time. The number of time units in which a behavior occurs depends on the temporal pattern of the behavior and on its duration.

It is clear from analyses of the data that certain states of behavior alternate with certain other states of behavior for particular durations. Here, a specific behavioral sequence is formed depending on time. Further, it may be true that the dominant behavior at any time has control over other types of activities as already stated by McFarland (1969); that, not only does the dominant system determine the time of occurence of the disinhibited activity, but it also determines its duration.

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BOOK REVIEW

Klama, J. *Aggression, the myth of the beast within.* (edited by J. Durant, P. Klopfer, and S. Oyama, from a text by J. Durant, E. Honore, L. Klopfer, M. Klopfer, P. Klopfer, T. Kohn, B. Lessley, N. Nur, and S. Oyama. New York: John Wiley & Sons, 1988.

"Beast knows beast; birds of a feather flock together." (Aristotle, Rhetoric, Book 1: 2:25

Aggression is a steady boarder at the table of the comparative psychologist, for it is a whale among the fishes in the sea of concepts that invite attention and resist identification and clarification. One reason for the confusion, these authors claim, is that the concept has both a "scientific image" and a "social reality" (p.2): it is time, the book argues, to change both. The past problem and the current danger, it is argued, is that analyses of aggression turn, tacitly or obviously, (it is the tacit that causes the problem) toward the "conclusion that beneath the superficially diverse range of phenomena embraced by the term there lies a unitary biological "base" — an aggressive "instinct" perhaps, whose origins may be traced far back in animal evolution." (p.6-7).

The "base" leads to the myth of the beast within. Here is a myth in both senses of the word: it is a false explanation, a myth in the sense that storks' delivering babies or Santa Claus is a myth; and it is a myth in the much larger and more interesting sense of the word; an idea that never makes itself perfectly evident but survives tucked away in our views of ourselves. The notion that human kind is basically sinful is an example of one such myth; and the notion that human beings are basically good is another.

Aggression is a complex myth (as are all the Great Myths), for our thoughts become twisted when we mix myths, as we are apt to do. For example, we cannot decide whether aggression is part of the human beings' good or evil self: like the image of the trickster in Jungian thought, it appears now one way, now another. We explain behavior by reference to aggression, but the explanation only reinvents the greatest and most troublesome myths of all; who are we, why are we here, and what ought we to be doing.

Having set this foundation, more or less, in Chapter 2 the book takes up brief reviews of the myths set forth by Darwin, Galton, Freud, Lorenz, and Mac Lean. Dawkins and sociobiology are given like, but untitled, attention and explanation. A section on the appropriate epistemology for understanding aggression is set forth in Chapter 3: this

section leads to a sensible discussion of questions that must be asked, questions that should not be asked, and the traps that appear between. The table being set, the full menu is now opened: these courses are chapters on cultural anthropology; genes, hormones, and learning in animals; human development, models of aggression, the evolution of conflict, and "Aggression revisited," Chapter 9, wherein, the reader might assume, the meal will settle.

Before we nibble more deeply into this promising offering, it is sensible to comment on the style of this book. The text, perhaps the first of its genre since the writing of the scriptures, is composed by having one set of editors rework the "a text" prepared by a larger group. The editors are among the larger group. The product is given a pseudonym.

The affect on this reviewer resembles an invitation to supper at which one is a stranger, but senses right away that the others have important relationships. The visitor is confused as to whom is related to whom, who knows whom; indeed, why anybody, in particular, is invited to the first place. There is a general topic, and all agree to speak to it. As the meal progresses, the conversation turns from the hosts' remarks to expositions by others. Sometimes, the listener suspects, others are speaking more to one another than to the topic. The result is that the guest devotes the energies to concentrated detective work in trying to understand the direction and plan of the discussion. The food is forgot, if it ever mattered, for the invitation was not truly to share. On second thought, the guest is a little annoyed at the suspicion of having been invited chiefly to admire the preening. Next morning, the guest awakes thoroughly confused, willing to consider him or herself a "bad" guest. Eventually, these feelings turn to further annoyance upon the realization that, most often, but not always, it is bad hosts who make bad guests.

Why do I think myself to have been a bad guest—an inconsiderate reader? The fault is not all mine. First, I now understand, the text speaks to itself: it is not truly directed to the reader, as occurs when an author truly wants the reader to understand. A good host strives to enjoin the guest in the conversation. No opportunity here: this guest is either talked around or lectured at. My hosts suggest, for example, that I have not paid sufficient attention to certain sets of studies, and descriptions without obvious purpose result. My hosts suggest that I am sufficiently insensitive to the evils of psychosurgery to be brought to task for my innocence. It is assumed that I lack the education or thought to grasp the myth of predestination. I am unlikely to know what Darwin really wrote, as my experience is certain to be second-hand. I am made to feel as a child at table, a table from my view composed of hordes of large and loud adults addressing one another, but not me — or rarely me.

The pity is that this book, surely in its opening chapters, understands that our studies of aggression is one way in which we invent myths

by which we understand ourselves. If this is not new ground, it is a welcome examination of an important and demythifying interpretation. The text here is informed: it is work of thoughtful scholarship. There is attention to the needs of the reader, as there is an honest attempt to inform and explain. Here is the work of a writer who is teacher, one who succeeds by wanting me to understand and learn. As is true of many a meal where there is too much wine, the text fails to keep the pace.

The writing now takes the style of the term paper: oddities creep into the text and crudities into the meal. For example, the discussion of Egas Moniz on 118-119 follows the argument and historical information set forth by Valenstein (1986), but the reference to Valenstein's work appears en passant on p.123 after a discussion of the work of Jose Delgado: a Scientific American format is suddenly adopted (p.117) as people are introduced as "a mid-Victorian neurologist; a Harvard physiologist, a Yale neurophysiologist, and a German neurophysiologist." Lorenz's model is repeated (p.26, 106), but not truly expanded, and we wonder how the explications are related? Freud's ideas, worthy of a major heading and discussion (23-25) rate this comment in the chapter on models — "Freud's ideas were expressed in metaphor and myth rather than in the operational terms of science, and it is at once pointless and presumptuous to dissect them in the current thinking about motivation." (p.110). Small matters, to be sure, but burps and belches during dinner nonetheless.

At times the reader is treated as mindless: the connection between phrenology and contemporary studies of brain localization is served up as some special dish, but no special point is made of it. This visitor's difficulty with Chapters 4-8 is simply that I leave each course uncertain as to what I am to understand that assists me in judging the argument of the initial chapters. It is one thing to admire a bird's coloration and display: it is quite another to grasp the meaning.

The final chapter, "Aggression revisited," which might finish the meal successfully, argues that "violence is still with us" (p.146) and takes up human rape, infanticide, and crime. The work ends, almost, with this "The conclusion to be drawn from our inquiry into the science and politics of aggression is not that there are pacific angels rather than aggressive monsters inside our heads." (p.155) And, a little later, "Can we keep our constructions of aggression where they belong, serving us as we strive to understand our own behaviour and that of other animals so as to improve the immediate and long-range prospects for us all? We can, but only if we resist the temptation to project our hopes and fears onto our scientific constructs." (p.155) The book concludes with such messages: they are wise ones: they may lead us to understand our own myths;

and they cannot be said too straightforwardly to all who would understand behavior and its origins.

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